JOURNAL OF AGRICULTURAL RESEARCH

VOL. XI WASHINGTON, D. C., DECEMBER 10, 1917 NO. 11

MOVEMENT OF SOLUBLE SALTS THROUGH SOILS

By M. M. McCOOL, *Professor of Soils*, and L. C. WHEETING, *Instructor in Soils, Michigan Agricultural Experiment Station*

INTRODUCTION

That there is a tendency for soluble materials to be distributed from regions of high to those of lower concentration in moist soils is to be expected from our knowledge of the phenomenon of diffusion. Moreover, it is generally recognized that the translocation is affected by moisture. One of us (McCool), while conducting soil cultural studies, has repeatedly observed that certain soluble salts when added to soils soon accumulate at or near the surface unless loss of water by evaporation is prevented. Moreover, it has recently been shown in our laboratories that the actual concentration of the soil solution induced by the addition of single salts required to inhibit the growth of higher plants, as well as to retard certain bacteriological activities in the soil, varies appreciably with different soils, which, of course, is to be predicted when we take cognizance of the exchange of bases that may result when salts are added to the soil, as reported by numerous investigators. Thus, during the progress of our researches on the concentration of the soil solution and related subjects several questions with respect to the movement of soluble salts in soils, as well as changes in the composition of the soil solution resulting from the addition of various substances, have arisen. Although reports concerning certain phases of the subject have been obtained, a critical examination of available literature has led to the conclusion that additional well-controlled experiments under both laboratory and field conditions are desirable. On account of the fundamental importance of this subject, the present status of the researches bearing upon it, and certain improved methods, it is being exhaustively investigated in our laboratories, as well as under field conditions. In this report, however, are presented results of some of our laboratory studies of the translocation of certain salts when added in varying amounts to soils of different texture and water contents, together with changes induced in the composition of the soil solution.

REVIEW OF LITERATURE

Müntz and Gaudechon,[1] several years ago conducted extensive experiments to determine the extent of the movement of sodium nitrate and potassium chlorid in soils, losses of water by evaporation being prevented. When crystals of sodium nitrate or potassium chlorid were placed in a light silicious soil of low water content, the soil containing the salt crystals gradually became moist at the expense of the surrounding soil. After eight days the changes in the water content of the soil receiving sodium nitrate were found to be as follows:

Effect of salt on water movement in the soil

	Per cent
Water content of soil when placed in container	3.2
Water content of soil containing a salt after 8 days	7.3
Water content of surrounding soil after 8 days	2.6

Moreover, seed were placed in the salted layer of soil and also in the surrounding mass. Germination was retarded in the one region by the high concentration of the soil solution, and in the other by lack of moisture. These authors maintain that when salt is added to a homogeneous mass of soil two systems result: One in which the vapor pressure is high and the other in which it is lower. As a result distillation of water takes place from the one to the other.

Analyses of samples of the soil taken at different distances from the point of application of the salts revealed that the movement of the same was negligible, even after 15 days. In another experiment a garden soil which contained 17½ per cent of water, spoken of as being quite moist, was also used as the medium. Under these conditions the distillation of water vapor did not take place; neither was the movement of the salts detected, 20 mm. from the point in which they were placed in the soil mass.

The extent of the vertical movement was determined by half filling a box 40 cm. high and 11 cm. thick with light soil containing 16 per cent of water, depositing 5 gm. of sodium nitrate, and then filling the box with the soil. The loss of water by evaporation was prevented. After three days samples were taken and the nitrate content was determined. Movement of the salt had not proceeded through a distance of 40 mm. Similar results were obtained with a soil somewhat more moist where determinations of the nitrate content were made six days after the experiment was set up.

Two glazed pots were filled with a sandy clay soil; one was gently, and the other heavily, compacted. Two gm. of powdered potassium chlorid were placed in the center of each, 15 mm. below the surface. Movement of the salt was found to have taken place to a slightly greater

[1] MÜNTZ, and GAUDECHON, H. DE LA DIFUSSION DES ENGRAIS SALINS DANS LA TERRE. *In* Ann. Sci. Agron., s. 3, anné 4, t. 1, no. 5, p. 379-411, 30 fig. 1909.

extent through the compacted soil, but even after one month it had not moved through a distance of 6 cm. Additional experiments with heavily compacted soils yielded data which show that compaction increases the movement somewhat; but even in heavily compacted soils the horizontal, as well as the vertical, movement is quite slow.

These authors also failed to detect more than a slight movement of salts, other than that induced by the percolation of water when soils to which were added the salts were exposed to 15.5 mm. of rain, or to which was applied water equal in amount to a rather heavy precipitation.

These authors conclude, as a result of their extensive studies, that certain fertilizer salts when placed in rather dry soils take up water from the surrounding soil and long remain localized in the humid area. As a result of this condition, seeds may not germinate; but this could be avoided by fertilizing and seeding at different intervals. When the soils are somewhat moist, the water movement does not take place; but, on the other hand, even in moist soils, the salts diffuse exceedingly slowly, on account of the discontinuity of the soil mass. Heavy compaction aids this movement, inasmuch as more particles are brought into intimate contact; yet in a very compacted soil the movement is slower than it is in free liquid. When salts are applied to soils under field conditions, they remain localized for long periods, although the rainfall may be appreciable.

Malpeaux and Lefort [1] report results of investigations of the movement of nitrates in a sandy and loam soil, respectively, under laboratory conditions. The soils were placed in tightly compacted wooden boxes about 50 cm. deep. In some cases the nitrates were placed in furrows in the soil, while in others the salt was deposited in holes made 3 cm. deep in the center of the boxes. It was found necessary to spray the soil with water several times during the experiment in order to replace that lost by evaporation. Samples of soil were taken at 5, 10, and 15 cm., distances both horizontally and vertically downward from the place of application of the nitrates. The authors bring out that the movement of salt by diffusion, either horizontally or vertically downward, is indeed slow. It seems that the translocation of the salts must have been affected by the movement of the water originally present in the soil, and by that added to it, from time to time, as evidenced by results of the next series.

Another series of experiments was carried on under field conditions. On July 13 nitrates were deposited 25, 50, 75, and 100 cm. from the surface of a loam soil. Samples were taken 8 cm. from the surface on July 24, August 13, and August 25, respectively, and the nitrates determined. The results obtained reveal that nitrates move upward quite rapidly, having traveled 40 cm. from the place of deposit after 31

[1] MALPEAUX, L., and LEFORT, G. LA CIRCULATION DES NITRATES DANS LE SOL. *In* Ann. Sci. Agron., s. 4, ann. 1, t. 2, no. 4, p. 241–258, 8 fig. 1912.

days. Between August 25 and October 25, 5.45 inches of rain fell. On October 25 samples of soil were taken at 10 cm. intervals from the surface to 100 cm. in depth. The nitrates were found to have been returned to lower levels by the rain water, but on the whole they were nearer the surface at the end of the period than they were at the beginning, the total rainfall amounting to 7.92 inches. These authors point out that nitrates would bring better results in many cases if they were turned under or applied very early in the season.

They[1] later continued the field experiments and studied the movements of nitrates in the soil by sampling and determining the nitrates present, and also by employing the sugar beet as the indicator. The previous field experiments were confirmed. The deep application of the nitrates afforded higher yields of beets than if they were placed nearer the surface.

Demolon and Brouet[2] consider that the mode of application of fertilizers should vary with the nature of the soil and with the cultural methods in vogue. In some cases part of the material should be applied in the autumn and the remainder in the spring when the seed bed is being prepared, and in others surface applications are desirable, and in still others plowing under is best. They maintain that salts have a general tendency to remain at the surface of the soil, rather large amounts of rain being required to carry nitrates into the subsoil.

FIG. 1.—Apparatus used in studying the movement of salts through soils.

There are on record results of numerous studies of the translocation of salts in soils induced by percolating water, Sharp[3] having made recent contributions. Jensen[4] has also shown that the solubility of certain inorganic constituents of the soil mass are increased by the presence of decaying organic matter; but, inasmuch as these do not bear directly upon our preliminary investigations, they are not considered at this time.

EXPERIMENTAL RESULTS

Usually brass tubes 1½ inches in diameter were employed as the containers in studying the movement of soluble salts in the soil, but in some of the early series glass cylinders 8 inches in length and 2 inches

[1] MALPEAUX, L., and LEFORT, G. LA CIRCULATION DES NITRATES DANS LE SOL; LEUR MODE D'EMPLOI. *In* Ann. Sci. Agron., s. 4, ann. 2, t. 2, no. 6, p. 705–726, 2 fig. 1913.

[2] DEMOLON, A., and BROUET, G. SUR LA PÉNÉTRATION DES ENGRAIS SOLUBLES DANS LES SOLS. *In* Ann. Sci. Agron., s. 3, ann. 6, t. 2, no. 6, p. 401–418, 2 fig. 1911.

[3] SHARP, L. T. FUNDAMENTAL INTERRELATIONSHIPS BETWEEN CERTAIN SOLUBLE SALTS AND SOIL COLLOIDS. *In* Univ. Cal. Pub. Agr. Sci., v. 1, no. 10, p. 291–339. 3 fig. 1916.

[4] JENSEN, C. A. EFFECT OF DECOMPOSING ORGANIC MATTER ON THE SOLUBILITY OF CERTAIN INORGANIC CONSTITUENTS OF THE SOIL. *In* Jour. Agr. Research, v. 9, no. 8, p. 253–268. 1917.

in diameter were used. As illustrated by figure 1; each of the brass containers was made up of three sections, the short central portions being 2 inches and each of the longer ones 8 inches in length. In setting up the series the short tubes were filled with the soil which had been treated with a definite amount of salt, the longer tubes joined to them, and then carefully filled with the moist untreated soil. The water content of the entire soil column was as nearly uniform throughout as could be made by careful mixing and screening. After the tubes were filled they were carefully sealed, unless otherwise specified, and then placed in a closed chamber, the temperature of which was maintained constant at 18° C. At the close of each period the tubes were unsealed; cross sections of the soil were removed by means of a spatula, dried, cooled in a desiccator, and carefully mixed; then the freezing-point lowering was determined in the usual manner.

MOVEMENT OF SOLUBLE SALTS THROUGH FINE-TEXTURED SOILS

In the first series of experiments the changes induced in the concentration of a rather heavy silt-loam-soil solution by the addition of sodium chlorid were studied. Water to the extent of 50 per cent of the oven-dry weight of the soil was added when the depressions of the freezing-point lowerings were determined. The results presented in Table I are quite striking, changes in the concentration of the soil solution being measurable 3 inches from the soil mass treated with 1 per cent sodium chlorid in solution, after seven days, and 2 inches from that receiving 0.1 of 1 per cent of the salt solution. Fifteen days after the treatment it is worthy to note that the concentration of the soil solution showed an increase throughout the tubes which had been treated with the larger amounts of sodium chlorid; but, on the other hand, changes induced in the soil which had received a more dilute salt solution were less striking. Under the above conditions the rate of salt movement becomes more rapid with an increase in the mass of salt added to the soil.

TABLE I.—*Changes in the concentration of the soil solution induced by the addition of sodium chlorid to a heavy silt loam*

Distance from salt layer.	Freezing-point lowerings.			
	After 7 days.		After 15 days.	
	1 per cent NaCl.	0.1 per cent NaCl.	1 per cent NaCl.	0.1 per cent NaCl.
Inches.				
4	0.000	0.000	0.025	0.000
3	.003	.000	.040	.000
2	.045	.006	.080	.010
1	.105	.010	.090	.020
0	.116	.015	.095	.010

Distance from salt layer.	Freezing-point lowerings.			
	After 5 days.		After 15 days.	
	1 per cent NaCl.	0.1 per cent NaCl.	1 per cent NaCl.	0.1 per cent NaCl.
Inches.				
1	0.100	0.012	0.075	0.013
2	.045	.....	.050	.005
3	.003	.000	.035	.000
4	.000	.000	.020	.000

In the next series of experiments another but lighter silt loam was used as the medium for studying the changes brought about in the concentration of the soil solution in the soil by the addition of sodium chlorid, 0.5 per cent of the salt was added in solution to 100 gm. of the soil, glass tubes being employed as the containers. An additional feature, notably the effect of different water contents upon the rate of change in the concentration of the soil solution, was included in this series.

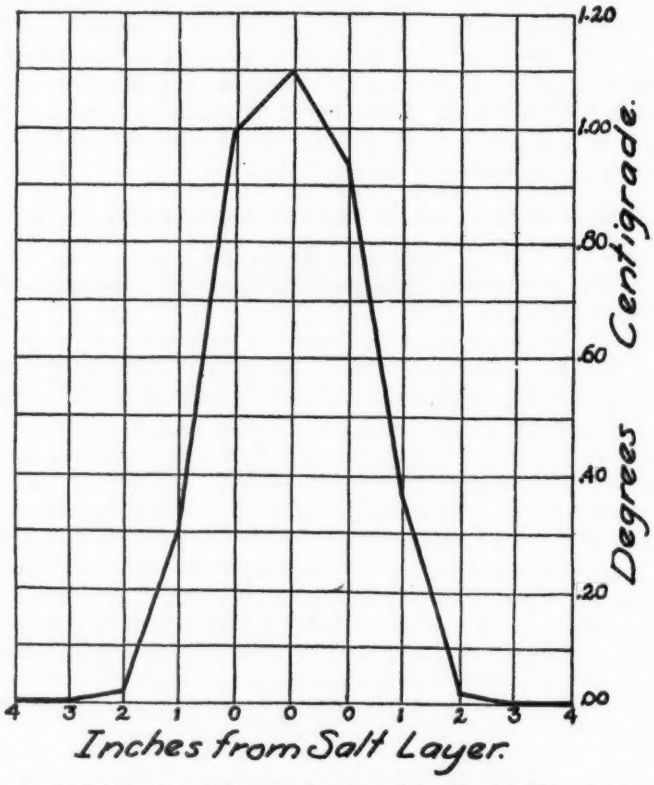


FIG. 2.—Graph of the freezing-point-lowerings after 5 days, induced by the addition of 2 per cent of potassium chlorid to silt loam with 20 per cent of moisture.

According to data presented in Table II, an increase in the concentration of the soil solution was measurable 2 inches from the salt layer after 5 days, becoming more apparent after 10 days; and at the close of the 20-day period the movement of the soluble material had taken place throughout the soil column. An examination of these data also reveals that the rate of movement through the soil containing 20 per cent of water was somewhat more rapid than it was through the soil which contained 10 per cent of water.

TABLE II.—*Changes in the concentration of the soil solution induced by the addition of 0.5 per cent of sodium chlorid to a light silt loam*

Distance from salt layer.	Freezing-point lowerings.					
	After 5 days.		After 10 days.		After 20 days.	
	10 per cent of water.	20 per cent of water.	10 per cent of water.	20 per cent of water.	10 per cent of water.	20 per cent of water.
Inches.						
3.....	0.000	0.000	0.000	0.000	0.022	0.100
2.....	.010	.040	.050	.130	.168	.160
1.....	.390	.350	.170	.160	.422	.230
0.....	.....	.....	.....	.....	.....	.....

Distance from salt layer.	Freezing-point lowerings.					
	After 5 days.		After 10 days.		After 20 days.	
	10 per cent of water.	20 per cent of water.	10 per cent of watre.	20 per cent of water.	10 per cent of water.	20 per cent of water.
Inches.						
1.....	0.430	0.380	0.390	0.350	0.480	0.260
2.....	.010	.110	.040	.130	.185	.180
3.....	.000	.020	.000	.010	.040	.070
4.....	.000	.000	.000	.000	.030	.020

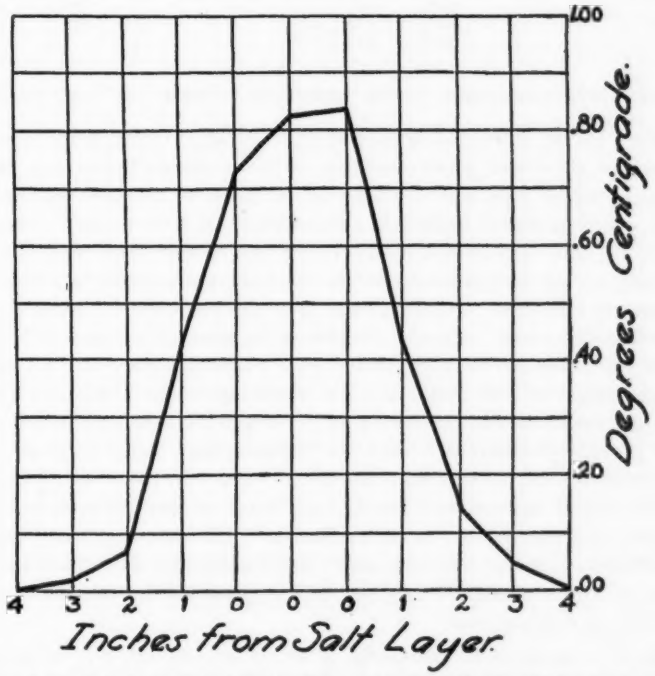


FIG. 3.—Graph of the freezing-point-lowerings after 10 days, induced by the addition of 2 per cent of potassium chlorid to silt loam with 20 per cent of moisture.

Potassium chlorid in solution amounting to 2 per cent of the treated layer of soil was added to the silt loam and the changes induced in the concentration of the soil solution in the soil were determined in the usual manner. The soil contained 20 per cent of water. The results obtained at the end of 5 and 10 day periods, respectively, are presented in Table III, and graphically shown in figures 2 and 3. Again changes in the con-

centration of the soil solution in the soil were measurable in the second layers of soil after 5 days, and at the end of 10 days movement had taken place throughout the soil mass in one case and to the third section in another.

TABLE III.—*Changes in concentration of the soil solution induced by the addition of 2 per cent of potassium chlorid to a silt loam with 20 per cent of water*

Distance from salt layer.	Freezing-point lowerings.		Distance from salt layer.	Freezing-point lowerings.	
	5 days.	10 days.		5 days.	10 days.
Inches.			*Inches.*		
4	0.000	0.000	0	0.930	0.840
3	.000	.018	1	.360	.435
2	.015	.070	2	.012	.135
1	.290	.425	3	.000	.050
0	.980	.720	4	.000	.010
0	1.100	.825			

MOVEMENT OF SOLUBLE SALTS THROUGH COARSE-TEXTURED SOILS

After having proved conclusively that an appreciable movement of salts from regions of greater to those of lesser concentration take place in fine-textured soils, it was considered advisable to continue the studies with coarse-textured materials. Accordingly a coarse grade (No. 1) of quartz sand was treated with 0.45 per cent of sodium chlorid, and the changes in the concentration in the various layers resulting from the treatment after 5-, 10-, and 20-day periods, respectively, were determined in the usual manner. In this series glass containers were employed, but instead of being placed in a horizontal position they were stood upright in the chamber. The results given in Table IV reveal that the upper movement after 5 days reached the first inch of soil and had progressed downward into the second inch. After 10 days the concentration of the solution was slightly greater in these sections than at the end of the previous period, and after 10 days' movement had progressed 1 inch farther in each direction. The more rapid downward movement, it seems, may be accounted for by the downward movement of water, inasmuch as 3 per cent approaches the maximum film capacity of this material.

TABLE IV.—*Changes in the concentration of the soil solution induced by the addition of 0.45 per cent of sodium chlorid to a coarse quartz sand with 3 per cent of water*

Distance from salt layer.	Freezing-point lowerings.			Distance from salt layer.	Freezing-point lowerings.		
	5 days.	10 days.	20 days.		5 days.	10 days.	20 days.
Inches.				*Inches.*			
4	0.000	0.000	0.000	1	0.140	0.130	0.015
3	.000	.000	.000	2	.060	.070	.020
2	.000	.000	.005	3	.000	.000	.010
1	.020	.040	.015	4	.000	.000	.000
0							

A fine grade of quartz was next employed, the material used being that which passed through a 40-mm. sieve. The salt used was 1 per cent potassium chlorid. The results presented in Table V show that the salt movement through this rather inert material is appreciable—that is, under the conditions of the experiment. The rate of translocation is more rapid than in the coarser material, probably on account of the greater number of points of contact in the fine quartz.

TABLE V.—*Changes in the concentration of the soil solution induced by the addition of 1 per cent of potassium chlorid to a fine quartz sand containing 5 per cent of water*

Distance from salt layer.	Freezing-point lowerings after 10 days.	Distance from salt layer.	Freezing-point lowerings after 10 days.
Inches.		*Inches.*	
4	0.000	1	0.335
3	.009	0	1.025
2	.075		

In the next and elaborate series a medium sandy soil was employed as the indicator. The effect of the mass of sodium chlorid added, as well as the water content upon the movement of salts in the soil, was studied. The data summarized in Table VI reveal that even within five days the concentration of the soil solution in the soil, which contained 3 per cent of water, was measureable in the second inch from the treated layer, and after 10 days in the third inch, and at the end of 20 days' movement was found to have progressed 4 inches. Where the water content of the soil was 9 per cent, the distance of movement was consistently greater at the end of each period, and it is notable that after 20 days the concentration of the soil solution in the last, or fifth, inch of soil, was comparatively great, or there seems to be a tendency under these and similar conditions toward a uniform concentration of the soil solution throughout the column of soil. Indeed, several preliminary experiments, which were continued about 75 days, showed this to be the case. Inasmuch as this phase of the subject is to be reported upon in detail later, these data are omitted.

TABLE VI.—*Changes in the concentration of the soil solution induced by the addition of 1 per cent of sodium chlorid to a medium sand*

Distance from salt layer.	Freezing-point lowerings.						Distance from salt layer.	Freezing-point lowerings.					
	3 per cent of water.			9 per cent of water.				3 per cent of water.			9 per cent of water.		
	5 days.	10 days.	20 days.	5 days.	10 days.	20 days.		5 days.	10 days.	20 days.	5 days.	10 days.	20 days.
Inches.							*Inches.*						
5	0.000	0.000	0.000	0.000	0.005	0.010	0	0.230	0.400	0.239	0.295	0.395	0.214
4	.000	.000	.007	.000	.010	.010	1	.130	.250	.160	.100	.155	.194
3	.000	.010	.033	.000	.015	.020	2	.010	.070	.065	.015	.025	.149
2	.005	.080	.098	.005	.055	.034	3	.000	.015	.004	.....	.017	.039
1	.180	.320	.183	.205	.225	.126	4	.000	.000	.002	.005	.010	.029
0	.210	.360	.259	.445	.245	.148	5	.000	.000	.000	.000	.005	.014
0	.250	.370	.316	.505	.405	.162							

In another series, reported in Table VII, 0.1 per cent of sodium chlorid in solution was added to a portion of the medium sand, in order to determine if the mass of salt present affects the rate of salt movement through sandy soil. It is obvious, from a comparison of the data with those in Table VI, that the movement becomes somewhat less rapid with the de crease in the amount of salt added to the soil. After 5 days the concentration of the soil solution in the first inch of soil was far less than it was in the previous series, and at the end of 10 days the increase in concentration of the soil solution was measurable in the second inch, whereas in the previous series the concentration had increased 5 inches from the salt layer.

TABLE VII.—*Changes in the concentration of the soil solution induced by the addition of 0.1 per cent of sodium chlorid to a medium sand*

Distance from salt layer.	Freezing-point lowerings.		Distance from salt layer.	Freezing-point lowerings.	
	5 days.	10 days.		5 days.	10 days.
Inches.			*Inches.*		
4	0.000	0.000	0	0.130	0.080
3	.000	.000	1	.018	.025
2	.000	.018	2	.000	.010
1	.025	.020	3	.000	.000
0	.085	.060	4	.000	.000
0	.140	.080			

Potassium chlorid was added to the medium sand, and the changes in the concentration of the soil solution in the soil were likewise determined after 5 and 10 days, respectively. The middle section of the brass tubes were filled with soil which had previously been treated with 0.9 per cent of the salt in solution, the moisture content of the entire soil column being 9 per cent. It is notable from Table VIII, and graphically represented in figures 4 and 5, that the concentration of the soil solution had increased in the first inch of soil after 5 days, and that the material in solution had passed into the third inch of soil after 10 days.

TABLE VIII.—*Changes in the concentration of the soil solution induced by the addition of 0.9 per cent of potassium chlorid to a medium sand containing 9 per cent of water*

Distance from salt layer.	Freezing-point lowerings.		Distance from salt layer.	Freezing-point lowerings.	
	5 days.	10 days.		5 days.	10 days.
Inches.			*Inches.*		
4	0.000	0.000	0	0.240	0.210
3	.000	.009	1	.090	.095
2	.000	.014	2	.000	.015
1	.075	.120	3	.000	.005
0	.265	.255	4	.000	.000
0	.260	.265			

In order to approach more nearly field-soil fertilization, 2 gm. of solid potassium chlorid and sodium carbonate, respectively, were placed in the middle of the tubes containing medium sand; otherwise the studies were conducted in the usual manner. The results presented in Table IX show that the concentration of the soil solution in the soil changes soon after solid salts are applied to the moist soils. The increase in the concentration within 5 days was appreciable 2 inches from the layer of potassium chlorid in the tubes containing 3 per cent of water, and 3 inches from it in those containing 9 per cent of water.

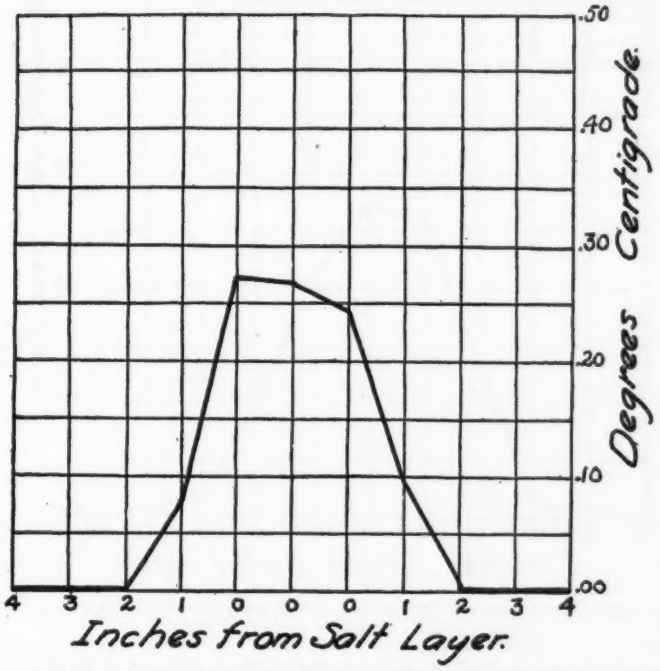


FIG. 4.—Graph of the freezing-point lowerings after 5 days, induced by the addition of 0.9 per cent of potassium chlorid to sand with 9 per cent of moisture.

TABLE IX.—*Changes in the concentration of the soil solution induced by the addition of 2 gm. of powdered potassium chlorid to a medium sand*

Distance from salt layer.	Freezing-point lowerings.				Distance from salt layer.	Freezing-point lowerings.			
	9 per cent of water.		3 per cent of water.			9 per cent of water.		3 per cent of water.	
	5 days.	15 days.	5 days.	15 days.		5 days.	15 days.	5 days.	15 days.
Inches.					*Inches.*				
4	0.000	0.085	0.000	0.003	1	0.650	0.368	0.255	0.282
3	.030	.251	.000	.096	2	.260	.335	.050	.141
2	.180	.493	.132	.214	3	.030	.117	.000	.113
1	.418	.691	.300	.277	4	.000	.067	.000	.005

It is notable that the changes induced by the addition of sodium carbonate were measurable after 5 days 1 inch from the salt in the soil containing 3 per cent and 2 inches from it where the moisture content was 9 per cent, and at the close of the 15-day period the soluble material had moved into the next layer of soil. The results obtained from the addition of this salt are given in Table X.

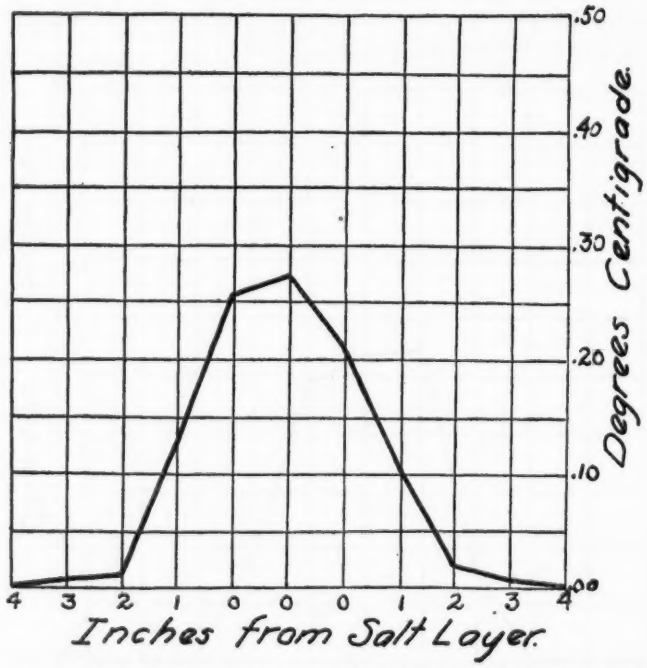


FIG. 5.—Graph of the freezing-point lowerings after 10 days, induced by the addition of 0.9 per cent of potassium chlorid to sand with 9 per cent of moisture.

TABLE X.—*Changes induced in the concentration of the soil solution by the addition of 2 gm. of powdered sodium carbonate to a medium sand*

Distance from salt layer.	Freezing-point lowerings.				Distance from salt layer.	Freezing-point lowerings.			
	9 per cent of water.		3 per cent of water.			9 per cent of water.		3 per cent of water.	
	5 days.	15 days.	5 days.	15 days.		5 days.	15 days.	5 days.	15 days.
Inches.					*Inches.*				
4	0.000	0.000	0.000	0.000	1	0.332	0.415	0.225	0.279
3	.000	.013	.000	.000	2	.025	.115	.005	.029
2	.029	.005	.000	.007	3	.000	.015	.000	.000
1	.349	.220	.303	.255	4	.000	.000	.000	.000

In another series the tubes were stood upright, the upper ends being open in order to permit loss of water by evaporation and to thus determine if the downward movement of the soluble material is appreciable when water is being lost in this manner. The results obtained and presented in Table XI show that the downward movement took place, the concentration of the solution being appreciably increased in the bottom layers of silt-loam soil, where 1 per cent of potassium chlorid was added, although the water content of the various layers was found to have decreased. It is possible that some of the soluble material in the lower layers would be translocated later on to the upper ones by the film water movement, this of course, could be determined by carrying on the experiments over a longer period. The greater concentration of the soil solution in the upper layers indicates an upward film movement of the water in this particular soil, of these water contents. We have experiments in progress which should show at what water content film movement ceases in different classes of soils.

TABLE XI.—*Movement of 1 per cent of potassium chlorid through silt-loam soil in open tubes, showing the concentration after 10 days*

Distance from salt layer.	Low moisture.			High moisture.			Distance from salt layer.	Low moisture.			High moisture.		
	Moisture content.	Moisture loss.	Freezing-point lowerings.	Moisture content.	Moisture loss.	Freezing-point lowerings.		Moisture content.	Moisture loss.	Freezing-point lowerings.	Moisture content.	Moisture loss.	Freezing-point lowerings.
Inches.							*Inches.*						
4.....	2.93	7.88	0.080	11.75	6.21	0.165	1.....	9.88	0.93	0.125	12.74	5.22	0.062
3.....	5.68	5.18	.065	11.95	6.01	.175	2.....	9.78	1.03	.038	12.64	5.32	.040
2.....	8.37	2.44	.110	12.21	5.75	.172	3.....	9.93	.88	.045	12.95	5.01	.058
1.....	8.85	1.96	.227	12.30	5.66	.130	4.....	10.02	.79	.060	13.00	4.96	.048
0.....	7.52	2.51	.270	12.00	5.96	.098							

Where sand was employed, rather strikingly different conditions have ensued. It may be cited that, for example, according to the data in Table XII, the amount of soluble material that moved downward was indeed slight in comparison with the upper translocation, or with the downward movement in the silt-loam soil. It is evident from these results that soluble salts such as sodium nitrate when applied to sandy soils, or present in them, are more likely to be lost to the crop by their accumulation in the upper layers of soil during a drouth than they are in case of the finer-textured classes of soils. Field experiments now under way may afford additional evidence bearing on this question.

TABLE XII.—*Movement of 1 per cent of potassium chlorid through medium sand in open tubes, showing the concentration after 10 days*

Distance from salt layer.	Low moisture.			High moisture.			Distance from salt layer.	Low moisture.			High moisture.		
	Moisture content.	Moisture loss.	Freezing-point lowerings.	Moisture content.	Moisture loss.	Freezing-point lowerings.		Moisture content.	Moisture loss.	Freezing-point lowerings.	Moisture content.	Moisture loss.	Freezing-point lowerings.
Inches.							*Inches.*						
4.....	0.46	2.73	0.048	3.68	4.69	0.285	1.....	2.25	0.94	0.020	4.73	2.95	0.018
3.....	1.23	1.96	.082	3.98	4.39	.045	2.....	2.37	.82	.007	4.82	3.55	.014
2.....	1.54	1.65	.090	4.11	4.26	.085	3.....	2.40	.79	.000	5.11	3.26	.002
1.....	2.00	1.19	.070	4.22	4.15	.050	4.....	2.45	.74	.000	5.30	3.07	.000
0.....	2.20	.99	.030	5.45	2.92	.013							

CHEMICAL STUDIES

Chemical studies of the solution obtained by extracting 1 part of the various layers of soil with 1 of distilled water and passing it through the Chamberland filter have been made. In the first series 300 gm. of medium sand and silt-loam soil, respectively, were treated with 1 per cent of sodium chlorid in solution, and were placed in the bottom of 3-gallon jars and the filling completed with untreated moist soils. One set was unsealed, in order to permit loss of water by evaporation. At the close of the experiment each 1-inch layer was air-dried, extracts obtained as above indicated, and certain bases determined. The depression of the freezing point of the soil and the amount of the bases found in the extraction are given in Table XIII.

TABLE XIII.—*Changes in the composition of the soil solution induced by the addition of 1 per cent of sodium chlorid to a medium sand and a silt loam. Duration, 15 days*

Distance from salt layer.	Medium sand, containing 9 per cent of water.				Silt loam, containing 20 per cent of water.			
	Freezing-point lowerings of soil.	Iron and aluminium.	Calcium.	Magnesium.	Freezing-point lowerings of soil.	Iron and aluminium.	Calcium.	Magnesium.
Inches.		*P. p. m.*	*P. p. m.*	*P. p. m.*		*P. p. m.*	*P. p. m.*	*P. p.*
4.....	0.042	No appreciable changes	+124.6	+6.90	0.002	No appreciable changes	+ 14.6	+ 5.58
3.....	.077		+ 74.3	+6.59	.050		+ 45.8	+11.50
2.....	.117		+ 51.7	+4.28	.322		+148.9	+19.95
1.....	.140		+ 26.7	+3.27	.522		+103.4	+12.70
0.....	.277		+ 39.4	+1.31	.687		+ 89.8	+ 9.47

It is notable that the addition of sodium chlorid resulted in an increase in the amount of the bases calcium and magnesium released to the solution upon extraction, the amount increasing from the salt-treated layer of soil upward in the case of the sand in the open con-

tainers. The magnesium and calcium were at the maximum in the second layer in case of the silt loam. The bases iron and aluminium were not measureably affected by the treatment.

The addition of the sodium carbonate, as may be seen from Table XIV, resulted differently, inasmuch as the amount of iron and aluminium in the extract from the treated and adjacent layers of sandy soil were strikingly increased, while the parts per million of calcium were appreciably less, and the magnesium decreased slightly in the two lower layers. In case of the silt loam the amount of calcium in the extraction from the treated and the adjacent layer of the soil was decreased, while the changes in the amount of magnesium were negligible.

TABLE XIV.—*Changes in the composition of the soil solution induced by the addition of 1 per cent of sodium carbonate to a medium sand and a silt loam. Duration of experiment, 15 days*

Distance from salt layer.	Medium sand, containing 9 per cent of water.				Silt loam, containing 20 per cent of water.			
	Freezing-point lowerings of soil.	Iron and aluminium.	Calcium.	Magnesium.	Freezing-point lowerings of soil.	Iron and aluminium.	Calcium.	Magnesium.
Inches.		*P. p. m.*	*P. p. m.*	*P. p. m.*		*P. p. m.*	*P. p. m.*	*P. p.*
4	0.004	0.00	+26.70	+2.75	0.000	No appreciable changes	+ 3.9	+1.74
3	.005	.00	+ 6.50	+1.14	.000		+ .8	.00
2	.053	+ 7.2	− 8.60	+ .61	.000		.00	.00
1	.257	+84.6	−10.00	− .15	.012		−14.5	.00
0	.287	+60.3	− 8.00	− .22	.092		−14.31	− .97

Where the containers were sealed, the presence of the sodium chlorid in medium-sand soil resulted in similar but somewhat less striking conditions than in the previous series. According to the data presented in Table XV, the amount of calcium and magnesium increased upward from the treated to the top layer, or these bases obviously were liberated to the soil solution and then passed onward to regions of lower concentration.

TABLE XV.—*Changes in the composition of the soil solution induced by the addition of 1 per cent of sodium chlorid and 1 per cent of sodium carbonate to medium sand. Duration of experiment, 25 days*

Distance from salt layer.	Sodium chlorid added.				Sodium carbonate added.			
	Freezing-point lowerings of soil.	Iron and aluminium.	Calcium.	Magnesium.	Freezing-point lowerings of soil.	Iron and aluminium.	Calcium.	Magnesium.
Inches.		*P. p. m.*	*P. p. m.*	*P. p. m.*		*P. p. m.*	*P. p. m.*	*P. p. m.*
3	0.002	+3.60	+ 3.60	+0.48	0.000	Trace.	+16.17	+0.92
2	.015	+3.40	+27.08	+4.21	.020	Trace.	+ 6.46	+ .39
1	.085	+1.20	+12.01	+1.79	.025	Trace.	− 4.65	− .44
0	.225	+4.60	+ 2.89	+ .26	.095	+63.00	− 3.46	+ .70

One per cent of sodium carbonate was added to a portion of the third layer of silt-loam soil taken from the closed containers and the second layer of sand, respectively. They were then moistened and let stand for five days in closed containers. At the end of this period the parts per million of the bases calcium and magnesium in the extracts were determined, the results obtained being given in Table XVI. It is notable that the addition of the sodium carbonate resulted in an appreciable decrease in the amount of these readily soluble bases, probably changing them from the chlorids to the carbonates.

TABLE XVI.—*Changes in the composition of the soil solution induced by the addition of sodium carbonate*

Soils.	Iron and aluminium.		Calcium.		Magnesium.	
	Before adding sodium carbonate.	After adding sodium carbonate.	Before adding sodium carbonate.	After adding sodium carbonate.	Before adding sodium carbonate.	After adding sodium carbonate.
		P. p. m.	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*
Silt loam	Trace.	70. 00	60. 50	16. 66	14. 43	6. 55
Sand	...do....	102. 00	61. 90	27. 76	6. 20	2. 79

DISCUSSION OF RESULTS

We have presented experimental data which show that soluble salts are translocated from regions of high to those of lower concentration in moist soils when inclosed in sealed containers; and in case of silt loam in the open containers upward movement is very rapid and the downward translocation is marked, the water movement evidently decreasing the downward translocation. We are at loss to account for the contradictory report of Müntz and Gaudechon, unless the methods employed failed to detect the changes that may have taken place in the nitrate content of the soil. In case of the potassium chlorid, the lack of movement reported may have been and probably was due to the retention of the potassium by the soil, other bases being forced into the solution.

As stated in the introduction, such movements are to be expected, especially if the moisture coats the soil particles in the form of films, in view of the fact that diffusion of salts take place in solution, but on the other hand the movement may not be and probably is not due wholly to diffusion. It does not seem untenable to assume that the reactions which take place when salts are added to the soil play their rôle. A given base coming in contact with a particle or a group of particles may be held and others liberated, adjacent particles may not be satisfied, so far as one or more of these bases are concerned, and by removing them from solution may aid in the translocation of soluble material in the soil.

The chemical studies show that the addition of soluble salts to a given region of the soil results in changes of the composition of the soil solution which may not be confined to the soil mass receiving the application. It seems that such conditions are of far-reaching importance in connection with the results obtained from the use of soluble-fertilizer salts, as well as attempts to bring about a so-called balanced soil solution. Inasmuch as soils undoubtedly vary with respect to the action that takes place when they are treated with various soluble substances, it does not seem possible to work out a balanced soil solution by studying a few soils.

CONCLUSIONS

(1) The results presented show that soluble salts move from regions of high to lower concentration in moist soils, the rate being rather rapid, and therefore do not long remain localized, as reported by earlier investigators. Moreover, the rate of movement is affected by the water content of the soil and the mass of salt present.

(2) Where moisture is being lost by evaporation, the upward movement is more rapid than the downward translocation in heavier soils; but in case of sands the downward translocation is indeed slight, thus indicating that soluble salts, such as sodium nitrate, are more likely to be lost by upward movement to the surface of sandy soils during a drought than in case of heavier soils.

(3) Chemical studies show that as the salts move through the soil mass the solution in the various layers of soil changes in composition. Such changes, it seems, have an important bearing upon the results to be obtained from the use of fertilizer salts, especially upon attempts to determine a so-called balanced soil solution by studies confined to a limited number of soils.

(4) The indications are that the translocation of soluble salts in soils is brought about by means of diffusion, by reactions that take place in the soil, and by moisture movements.

(5) Field and laboratory experiments in progress should throw additional light upon moisture movement in different soil classes, as well as the upward movement from the subsoil of substances in solution.

23717°—17——2

BREEDING SWEET CORN RESISTANT TO THE CORN EARWORM

By G. N. COLLINS, *Botanist*, and J. H. KEMPTON, *Scientific Assistant*, *Office of Acclimatization and Adaptation of Crop Plants and Cotton Breeding, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

The production of sweet corn (*Zea mays*) in the southern part of the United States and throughout the American Tropics is seriously interfered with by the ravages of the corn earworm (*Chloridea obsoleta* Fab.).

The geographic range of this insect is practically coextensive with maize culture, extending to the northern boundaries of the United States. But Quaintance and Brues[1] state that nowhere in the transition zone, comprising in the main the New England States, New York, Pennsylvania, Michigan, Wisconsin, and Minnesota, is the pest of regular occurrence or a cause of any considerable damage. For some distance south of this region the injury is also comparatively slight, but in many sections near the southern border of the country sweet corn is not grown at all, its place on the table being taken by field varieties.

The exclusion of sweet varieties from these regions may not be entirely due to the corn earworm, but it is probably safe to consider this insect the major factor.

The corn earworm does not confine its depredations to sweet corn, but also attacks field varieties. From the fact that northern varieties of field corn, when grown in the South suffer much more than do the local sorts, it would appear that the especial susceptibility of sweet varieties is not due to the character of the seeds alone, and that the southern varieties of field corn must possess some additional peculiarity that renders them at least partially immune.

A comparison of the general characteristics of northern and southern varieties at once suggests that the greater immunity of southern varieties may be due to the greater development of husks in the southern varieties. Attention was early called to this possibility by Mr. O. F. Cook,[2] from observations made on a variety of corn growing near Brownsville, Tex. This variety produces small ears inclosed in very long husks. Mr. Cook noticed that, while many larvæ were found inside of the projecting husks, few had reached the ears.

[1] QUAINTANCE, A. L., and BRUES, C. T. THE COTTON BOLLWORM. U. S. Dept. Agr. Bur. Ent. Bul. 50, 155 p., 27 fig., 25 pl., 1905.

[2] Bionomist in Charge, Office of Acclimatization and Adaptation of Crop Plants and Cotton Breeding, Bureau of Plant Industry.

Journal of Agricultural Research,
Washington, D. C.
lc

Vol. XI, No. 11
Dec. 10, 1917
Key No. G—129

With the idea that southern field varieties owe their relative immunity to the thick covering of long husks which protect their ears, it seemed worth while to endeavor to breed varieties of sweet corn possessing numerous long husks. Since the distinctive character of the seeds of sweet varieties behaves in hybrids as a Mendelian unit, strains that would breed true to the sweet character might be expected in the second generation of a cross between field and sweet varieties. It was hoped that from the plants producing sweet seeds, strains possessing the desired husk characters could be isolated.

The present paper is an account of an attempt to secure this result, with a discussion of some of the factors of worm resistance on which light has been thrown in the course of the experiment.

Even in the worst worm-infested regions it is largely a matter of chance whether any particular ear is injured or escapes. To select intelligently, it is therefore highly important to know something of the plant characters that minimize injury and to use these characters as a basis for selection. The study of the characters associated with worm resistance was carried on simultaneously with the breeding work, and the value of the results is believed to lie in the analysis of the characters and the method of breeding quite as much as in the material results. These material results comprise two strains of sweet corn possessing marked resistance to the corn earworm.

PROTECTIVE CHARACTERS

Four protective characters were in mind at the beginning of the experiment: (1) The distance which the husks extend beyond the tip of the ear, with the idea that larvæ frequently gain access to the ear by entering at the tip of the shoot and eating their way down the silks. It would obviously be advantageous to increase the distance they must travel. (2) The thickness of the husks' covering. Many ears are found with perforations through the husks, and a thicker covering might be expected to hinder the invasion of the larvæ from this direction. (3) The texture of the husks. In most sweet varieties the husks are relatively soft and smooth, while in field varieties, especially those from the Tropics, the husks are firm and harsh. The outer husks of some varieties are covered with firm spicules, providing a surface almost as silicious as sandpaper. This character might be expected to deter the insects from eating their way to the ear through the husks. (4) Husk leaves. It was thought that ears without husk leaves might be less attractive to moths.

PLAN OF EXPERIMENTS

The experiments were begun in 1912. Mr. John H. Kinsler, at Victoria, Tex., made various crosses between three commercial varieties of sweet corn, Stowell's Evergreen, Early Evergreen, and Early Cory, and two varieties of field corn, Brownsville and Marrainto. Brownsville is

a selected strain of the variety in which Mr. O. F. Cook had first observed the worm resistance; Marrainto is a variety from northern Mexico, with rather thicker and harsher husks than those of Brownsville. These also extend well beyond the ear.

Isolated plantings of the first generation of these crosses were made at Victoria in 1913. The four lines which have been continued are Ph75 Brownsville × Early Cory; Ph77 Early Evergreen × Brownsville; Ph79, Stowell × Brownsville; and Ph80, Marrainto × Evergreen. The ears from the first-generation hybrid plants contained a mixture of sweet and horny seeds. The sweet seeds from selected ears of each of the four hybrids were planted in separate rows at Lanham, Md., in 1914, one row from each ear.

The procedure in 1914 was to make pollinations between plants of a similar appearance, and usually within the same row. The distance the husks extended beyond the ear, the thickness and number of husks, and the extent to which husk leaves were developed were recorded for all plants used in making pollinations. An attempt was also made to grade the plant with respect to the texture of the husks.[1] In selecting plants for pollination preference was given to those with long husks and few husk leaves; but other types were also pollinated, including a few that were distinctly inferior with respect to the characters thought to denote worm resistance.

Fourteen ears were selected for ear-to-row tests in 1915. The designations of these ears with their ancestry are given in Table I.

TABLE I.—*History of the corn plantings made at Chula Vista, Cal., in 1915*

1912. Victoria, Tex. Original cross.	1913. Victoria, Tex. Treatment.	1914. Lanham, Md. (Sweet seeds planted.) Plant combinations.	1915. Chula Vista, Cal. Planting designation.
Brownsville × Early Cory	Isolated block	121×122	Ph121
Do	do	124×122	Ph123
Do	do	1×9	Ph127
Do	do	8×111	Ph128
Evergreen × Brownsville	Hand-pollinated	10×12	Ph129
Do	do	12×10	Ph130
Do	do	12×15	Ph131
Stowells × Brownsville	Isolated block	159×158	Ph120
Do	do	137×75	Ph122
Do	do	140×138	Ph124
Do	do	89×30	Ph125
Do	do	162×160	Ph126
Marrainto × Evergreen	Hand-pollinated	182×179	Ph118
Evergreen × Brownsville	do	32 × 21	
Stowells × Brownsville	Isolated block		Ph119

[1] The surface of the husks in the hybrid progenies is distinctly harsher than in commercial varieties of sweet corn. It was not found possible, however, to distinguish the different progenies in this particular with serviceable accuracy and the notation of the character has been discontinued.

The 1915 planting was made at Chula Vista, near San Diego, Cal., on March 15. The corn earworm is a more serious pest in this region than at Lanham, Md., and a more uniform infestation resulted.

In comparison with other plantings of sweet varieties in the same neighborhood, there seemed little doubt that the field of hybrids as a whole was less injured than other varieties. An effort was made, however, to secure definite quantitative data on the effect of the selection, and to determine the characters most closely associated with immunity. The characters of the individual plants were recorded in a series of measurements described below:

(1) DAMAGE.—The portion of the ear rendered inedible was estimated on a scale of 10—that is, an ear in which the larvæ had eaten completely to the base, rendering it worthless, was classed as 10. The slightest damage was recorded as 1 and an ear one-half of which was destroyed as 5. With intermediate stages estimated on the same scale, the grading was all done by the junior author and experiments showed that the maximum uncertainty regarding the class to which any particular ear should be referred was not greater than one grade.

(2) NUMBER OF LARVÆ.—The number of larvæ found inside the husks at harvest, together with any which it could be seen had escaped. When the infestation is very severe, the fact that the larvæ are cannibalistic would doubtless cause the recorded number to be lower than the true number.

(3) DAMAGE PER LARVA.—The figure indicating the total damage of each progeny divided by the total number of larvæ in the same progeny.

(4) PROLONGATION.—The distance from the tip of the ear to the tip of the husks, recorded in centimeters.

(5) LENGTH OF HUSKS.—This measurement was obtained by adding the prolongation and length of ear.

(6) LENGTH OF EAR.—The length of the ear in centimeters, including any damaged portion.

(7) NUMBER OF HUSKS.—The total number of husks surrounding the ear.

(8) NUMBER OF LAYERS.—A small hole was cut through the husks at the side of the ear at a point about midway between the tip and the base, and the number of layers of husks at this point were recorded.

(9) DAYS TO SILKING.—The number of days that elapsed from planting to the first appearance of silk.

(10) MATURITY.[1]—The degree of maturity was judged by slicing off the tops of the grains, and estimating the proportion of opaque to transparent endosperm. Prime eating condition was designated "grade 10." The lowest grade that would be marketable on our scale would be about 6 and the highest about 15.

(11) SILKING TO HARVEST.[1]—The number of days that elapsed between silking and harvesting of the ear.

(12) HUSK LEAVES.—The extent to which husk leaves were developed was graded in accordance with an arbitrary scale ranging from 0 to 10. The same system of grading husk leaves has been used for a number of years in recording the behavior of all varieties grown and has proved to be a reliable measurement.

(13) NUMBER OF ROWS.—The number of rows of grains on the ear was included in the notes largely as an indication of the circumference of the ear.

Table II gives the mean value of each of the characters for each of the progenies grown in 1915.

[1] Not taken in 1915.

TABLE II.—*Measurement of plant characters at Chula Vista, Cal., in 1915*

Progeny.	Damage.		Number of larvæ.		Damage per larva.		Prolongation.	
	First ears.	Second ears.	First ears.	Second ears.	First ears.	Second ears.	First ears.	Second ears.
Ph118	2.1±0.3	3.1±0.3	1.3±0.1	1.4±0.1	1.7±0.3	2.1±0.2	9.8±0.6	9.9±0.4
Ph119	2.7± .3	1.6± .2	1.6± .2	1.2± .1	1.7± .3	1.3± .2	9.7± .5	10.9± .5
Ph120	3.3± .6	1.9± .4	1.7± .2	1.2± .1	2.0± .5	1.5± .3	9.8± .6	9.8± .8
Ph121	2.5± .3	1.6± .2	1.8± .2	1.5± .1	1.4± .2	1.1± .2	9.7± .2	9.8± .5
Ph122	2.2± .2	1.4± .3	1.4± .1	1.3± .1	1.5± .2	1.1± .2	11.2± .3	11.6± .8
Ph123	1.8± .3	1.5± .3	1.3± .1	1.3± .1	1.4± .9	1.2± .2	8.3± .4	8.7± .5
Ph124	.8± .2	1.9± .5	1.1± .1	.8± .1	.7± .2	2.3± .8	13.1± .6	11.9± .8
Ph125	5.9± .8	4.6± .8	2.2± .1	2.0± .2	2.8± .4	2.3± .4	9.7± .5	8.1± .8
Ph126	3.1± .3	4.4± .7	2.1± .1	1.8± .3	1.5± .2	2.4± .5	6.5± .4	7.8± .9
Ph127	3.3± .5	4.3± .4	1.9± .2	2.1± .1	1.8± .3	2.1± .2	6.0± .7	5.2± .4
Ph128	5.0± .8	3.1± .3	2.1± .1	1.8± .2	2.4± .4	1.7± .3	12.5± .6	11.9± .7
Ph129	5.3±1.1	4.4± .8	2.3± .2	1.7± .2	2.3± .5	2.6± .5	7.7± .1	10.3± .7
Ph130	3.1± .4	2.7± .3	1.7± .2	1.9± .2	1.9± .4	1.4± .2	8.9± .5	8.4± .4
Ph131	3.8± .4	2.4± .3	1.9± .1	1.5± .1	2.0± .2	1.6± .2	7.3± .5	10.1± .6

Progeny.	Length of ear, first ears.	Number of husks, first ears.	Number of layers.		Days to silking, first ears.	Husk leaves.		Number of rows, first ears.
			First ears.	Second ears.		First ears.	Second ears.	
Ph118	13.1±0.3	12.7±0.3	10.7±0.3	10.0±0.2	98±1	2.8±0.3	3.3±0.2	14.0±0.2
Ph119	14.7± .3	13.3± .4	10.0± .3	10.4± .3	108±1	.6± .1	1.5± .2	15.0± .3
Ph120	14.3± .5	16.4± .7	11.6± .4	12.2± .4	113±2	2.2± .4	2.7± .3	16.7± .4
Ph121	14.3± .3	12.3± .4	8.8± .4	7.9± .3	107±1	4.3± .3	4.8± .4	12.4± .2
Ph122	15.8± .3	14.1± .3	10.9± .2	12.2± .3	107±1	.4± .1	.9± .2	13.0± .2
Ph123	15.4± .3	12.4± .3	10.6± .4	10.3± .2	105±1	1.8± .3	2.3± .2	13.2± .3
Ph124	15.3± .4	13.7± .4	11.6± .5	10.9± .3	111±2	.3± .2	1.2± .2	17.1± .4
Ph125	15.6± .6	10.1± .4	8.7± .3	9.2± .9	96±2	1.1± .3	1.0± .3	14.8± .3
Ph126	15.1± .5	12.8± .4	10.2± .4	12.1± .7	115±1	1.8± .3	1.6± .4	17.5± .5
Ph127	11.9± .6	10.8± .6	7.3± .2	7.1± .5	104±3	1.4± .4	3.7± .5	13.6± .4
Ph128	12.3± .4	11.7± .6	7.8± .5	8.4± .3	107±2	1.4± .4	2.8± .4	14.5± .2
Ph129	14.7± .8	15.0± .4	10.0± .4	9.3± .5	92±4	.7± .4	1.6± .2	15.3± .5
Ph130	14.3± .3	14.7± .6	10.0± .2	9.4± .2	90±1	1.2± .2	3.9± .3	14.7± .3
Ph131	14.0± .5	12.8± .6	9.1± .3	9.4± .3	103±2	1.2± .1	3.0± .3	13.1± .2

ANALYSIS OF RESULTS IN 1915

The first step in analyzing the results was to determine whether the several rows showed real differences in the amount of damage inflicted by the corn earworm. If significant differences were not developed, it would hardly be worth while to proceed with selection.

The average damage for the different rows is shown in columns 2 and 3, Table II, together with the probable errors. It will be seen that some rows are damaged much more than others, and a consideration of the probable error shows that many of these differences may not be ascribed to chance. An analysis of the first, or upper ears, for which the data are more complete, shows that the row with the greatest amount of damage, Ph125, was damaged seven and one-half times as much as Ph124, which was the least affected.

It was thought possible that the degree of damage of the different rows might be influenced by their position in the field. The infestation might come from one side of the field and the rows nearest its source thus be more severely damaged. The arrangement of the progenies in the table corresponds with that in the field, and no general trend is apparent. It hap-

pens that the least and most damaged rows stood side by side near the middle of the field. If location was a factor, adjacent rows should, on the average, show a closer agreement in the extent of damage than pairs taken at random. On eliminating Ph129, which is the reciprocal of Ph130, the correlation between adjacent rows for the upper ears alone is 0.161 ±0.189 and for upper and second ears combined 0.173±0.189. There is, thus, little or no tendency for adjacent rows to be damaged to a similar extent, and position in the field seems not to be an important factor in causing the observed differences.

On the other hand, if the immunity which some of the rows enjoyed is due to plant characteristics, there should be some agreement between the degree of immunity of upper and second ears of the same row. A comparison of the value in columns 2 and 3, Table II, shows such an agreement. The row in which the upper ears were most damaged is also the row in which the second ears were most damaged. It can also be seen that the row with the least damage to the first ears has a very low damage in the second ears. Beyond these rather outstanding cases, the agreement or lack of agreement is not obvious from inspection. The correlation of damage between upper and second ears is believed to be a fair measure of this agreement; it was found to be 0.718±0.087. This correlation alone would seem to establish the fact that the individuality of progenies is an important factor in determining the extent of damage. From the 1915 results we may safely conclude that there is something about the plants descended from certain ears which affords them an appreciable measure of protection. The next step was to determine, if possible, whether this protection could be referred to any of the recorded plant characters.

As soon as a detailed analysis of the 1915 data was attempted it became evident that there were sources of error that had not been adequately guarded against. The ears were not harvested at a uniform stage of development, and those left longer were more severely damaged. There were also many ears bagged to secure pure seed, and since the bagging was in a measure selective, it introduced another source of possible error. These disturbing factors made it appear unwise to place confidence in any detailed analysis of the 1915 data. These results will therefore be considered only in connection with the results of the following season.

EXPERIMENTS IN 1916

The 1916 plantings were made at Lanham, Md., on May 14 and consisted of 35 rows, as follows: A repetition of the 14 progenies grown in 1915 (ancestry described on p. 551), 9 progenies from ears secured by hand pollinations within the rows of the progenies grown in 1915, 8 progenies from ears obtained by crosses between the rows in 1915, and 2 first-generation crosses between 1915 progenies and Hopi maize. There were

also included one row of Oregon Evergreen (P129), a commercial variety of sweet corn, and a row of New Century Wonder (P125), a commercial soft variety on the market as a table corn. The pedigrees of the progenies added to the 14 progenies that were repeated from 1915 are given in Table III.

TABLE III.—*Ancestry of progenies added to the experiment in 1916*

1916 designation of progeny.	Nature of pollination in 1915.			
	Pistillate parent.		Staminate parent.	
	Plant No.	Progeny.	Plant No.	Progeny.
Ph119C1	3308	Ph119	Self.	.....
Ph123C1	3529	Ph123	3523	Ph123
Ph125C1	3609	Ph125	3603	Ph125
Ph125C2	3625	Ph125	3617	Ph125
Ph127C1	3718	Ph127	3706	Ph127
Ph128C1	3776	Ph128	3773	Ph128
Ph128C2	3773	Ph128	3754	Ph128
Ph130C1	3865	Ph130	Self.	.....
Ph132	3270	Ph118	3323	Ph119
Ph133	3330	Ph119	3601	Ph125
Ph134	3334	Ph119	3286	Ph118
Ph135	3368	Ph120	3328	Ph119
Ph136	3369	Ph120	3328	Ph119
Ph137	3373	Ph120	21	Hopi.
Ph138	3403	Ph121	3328	Ph119
Ph139	3489	Ph122	3320	Ph119
Ph140	3557	Ph124	3523	Ph123
Ph141	3602	Ph125	21	Hopi.

The method of taking notes has already been described (p. 552). The same procedure was followed as in 1915, except that the number of days from silking to harvest and the degree of maturity were added.

To make it possible to secure ears at approximately the same degree of maturity, the exact dates of the first pollen and the first appearance of silks were recorded on a tag attached to each plant. After a few preliminary experiments it was found that from 16 to 18 days after silking the ears were in prime eating condition. The attempt was made, therefore, to harvest all ears within these dates. There was some deviation from this rule, but the results showed that these departures did not materially affect the damage.

Table IV gives the mean values of the characters (first and second ears combined) for each of the progenies, with the probable errors of the determinations. As in 1915, the order of the progenies in the table is the same as that in which they were planted.

The 14 original progenies, which are repetitions of the 1915 series, are marked with an asterisk. The 1915 ancestry of the new progenies is given in Table III, but to trace the ancestry back of 1915 reference may be made to Table I.

TABLE IV.—*Mean of different characters of corn, first and second years combined, in 1916*

Progeny.	Number of plants.	Damage.	Number of larvæ.	Damage per larva.	Prolongation.	Length of husks.	Length of ear.	Number of husks.	Number of layers.	Days to silking.	Maturity.	Days silking to harvest.	Husk leaves.	Number of rows.
		Grades.		*Grades.*	*Cm.*	*Cm.*	*Cm.*				*Grades.*		*Grades.*	
P125	79	0.63±0.07	0.72±0.04	1.14±0.15	*3.75±0.27	28.9±0.24	25.0±0.21	11.4±0.19	9.31±0.14	89.0±0.35	12.0±0.17	18.9±0.23	2.29±0.12	12.3±0.11
P129	47	1.11± .10	.89± .06	1.24± .14	5.61± .48	26.1± .46	26.2± .39	13.8± .30	7.68± .13	80.9± .36	9.7± .18	16.4± .08	5.42± .20	13.8± .15
*Ph118	64	.50± .08	.72± .04	.70± .12	7.14± .19	25.2± .24	18.2± .24	13.0± .16	9.67± .21	85.0± .34	11.5± .13	17.7± .11	4.53± .18	13.6± .13
*Ph119	68	.28± .05	.60± .04	.46± .14	8.75± .36	27.4± .32	18.8± .19	13.9± .22	9.65± .17	82.2± .32	10.1± .14	17.2± .14	2.95± .14	15.3± .15
Ph119C1	47	.47± .09	.62± .06	.76± .20	10.20± .47	25.6± .25	15.2± .22	11.0± .20	8.20± .16	80.7± .18	9.4± .22	16.4± .57	1.68± .18	12.4± .14
*Ph120	51	.39± .09	.76± .04	.51± .12	7.57± .33	27.6± .33	20.1± .25	15.5± .32	11.20± .15	87.0± .42	11.1± .14	17.2± .14	2.10± .13	17.6± .22
*Ph121	65	.97± .06	.86± .03	1.12± .08	4.06± .28	24.8± .24	21.0± .17	15.5± .21	10.60± .16	84.3± .34	10.9± .12	17.1± .16	4.10± .14	13.5± .19
*Ph122	71	.51± .07	.76± .03	.67± .09	5.50± .30	26.8± .27	21.5± .20	15.2± .20	10.60± .14	84.4± .28	10.6± .11	17.2± .06	2.53± .14	14.2± .12
*Ph123	66	.58± .07	.68± .05	.85± .13	5.06± .30	25.5± .21	20.3± .19	11.9± .16	9.57± .15	83.6± .38	10.7± .09	16.8± .08	2.40± .10	13.1± .13
Ph123C1	55	.76± .06	.87± .04	.88± .08	2.38± .25	22.9± .22	20.2± .20	11.1± .18	8.30± .15	84.0± .33	11.0± .11	16.8± .10	2.96± .12	12.1± .09
*Ph124	27	.04± .01	.37± .10	.10± .03	10.80± .43	30.4± .43	19.0± .30	14.7± .32	1.12± .24	85.3± .48	10.5± .15	17.2± .09	1.37± .10	18.3± .32
*Ph125	44	.45± .08	1.02± .06	.45± .09	8.04± .58	29.0± .34	21.3± .50	11.9± .27	9.10± .19	79.0± .44	10.6± .27	16.3± .06	5.73± .23	15.3± .23
Ph125C1	63	.71± .08	.84± .05	.85± .11	6.76± .25	26.8± .25	20.0± .26	12.6± .20	8.90± .16	78.0± .38	9.8± .13	16.6± .08	4.85± .22	15.1± .24
Ph125C2	22	1.00± .18	.96± .08	1.05± .20	4.68± .50	26.9± .58	22.4± .34	12.1± .29	8.90± .31	83.0± .84	10.1± .34	17.1± .23	2.77± .30	15.4± .36
*Ph126	55	.91± .08	.73± .05	1.25± .15	3.68± .27	24.3± .24	20.2± .35	11.9± .21	8.84± .18	90.1± .53	12.4± .29	19.3± .34	3.12± .13	17.3± .10
*Ph127	67	1.19± .09	1.13± .07	1.04± .10	2.94± .22	22.9± .25	19.6± .24	13.2± .19	8.20± .15	79.0± .38	9.5± .11	16.4± .06	5.30± .18	14.7± .17
Ph127C1	45	1.93± .18	1.18± .08	1.64± .20	2.69± .32	21.9± .39	18.8± .23	13.1± .21	7.87± .17	78.4± .52	9.8± .16	16.5± .05	3.69± .13	14.9± .23
*Ph128	86	.45± .06	.65± .04	.70± .11	9.16± .31	30.4± .26	21.2± .21	13.3± .20	9.70± .14	81.0± .27	10.6± .12	17.2± .14	4.14± .15	16.3± .14
Ph128C1	70	.29± .09	.52± .06	.56± .19	12.00± .29	29.9± .33	18.1± .19	13.8± .23	9.09± .15	83.0± .43	10.9± .12	17.4± .10	3.50± .18	15.7± .17
Ph128C2	18	1.39± .31	.95± .11	1.47± .37	11.60± .76	31.6± .57	19.8± .32	13.4± .28	10.20± .28	80.9± .82	10.4± .19	16.5± .11	3.56± .20	15.5± .43
*Ph129	54	1.13± .10	1.11± .07	1.01± .11	5.05± .22	24.0± .26	19.0± .22	13.3± .21	8.76± .18	75.1± .30	9.4± .14	16.1± .02	4.93± .26	15.6± .22
*Ph130	85	1.10± .07	1.14± .04	.97± .07	5.40± .20	24.4± .24	19.0± .20	14.6± .18	9.15± .15	74.5± .27	8.8± .16	15.9± .08	5.71± .20	15.6± .14
Ph130C1	70	.95± .08	1.03± .04	.92± .09	6.70± .27	22.7± .25	15.8± .24	13.1± .16	8.95± .14	75.7± .37	9.2± .14	16.1± .04	4.27± .22	16.3± .10
Ph130C2	78	.87± .05	.99± .03	.88± .06	5.97± .26	25.1± .19	19.0± .21	12.6± .16	8.80± .14	76.7± .26	9.8± .03	16.6± .09	3.90± .19	16.6± .14
*Ph131	68	.96± .08	1.15± .03	.83± .07	5.95± .25	24.3± .19	18.3± .21	15.1± .22	9.50± .16	74.2± .25	8.6± .16	15.9± .09	4.22± .20	14.9± .15
Ph132	99	.33± .03	.50± .05	.67± .14	7.65± .22	25.8± .27	18.2± .14	12.1± .14	8.64± .12	79.1± .26	10.4± .06	16.6± .06	4.10± .14	13.9± .11
Ph133	35	.34± .05	.71± .07	.50± .19	6.80± .38	28.9± .42	22.1± .32	13.3± .34	9.82± .24	81.0± .64	9.3± .27	16.7± .14	4.34± .30	15.8± .20
Ph134	67	.36± .03	.52± .06	.69± .20	10.30± .30	27.9± .30	17.6± .22	13.9± .20	10.40± .16	79.8± .34	10.3± .07	16.4± .04	3.58± .21	14.0± .15
Ph135	62	.65± .08	.65± .04	1.00± .14	4.10± .24	24.5± .22	20.4± .18	17.7± .35	12.10± .19	83.8± .32	10.9± .14	17.3± .15	2.59± .13	16.4± .19
Ph136	30	.57± .11	.67± .06	.85± .18	5.16± .47	24.0± .37	18.5± .23	17.2± .45	10.70± .36	84.2± .45	11.1± .11	17.2± .13	2.80± .22	15.7± .32
Ph137	60	1.37± .10	1.11± .05	1.22± .11	5.06± .33	27.4± .27	22.6± .36	15.6± .28	9.70± .18	78.1± .37	10.6± .15	17.4± .18	4.20± .17	18.3± .17
Ph138	91	.74± .06	.66± .04	1.11± .11	3.04± .22	26.1± .21	23.1± .17	16.3± .20	10.80± .14	83.8± .27	11.2± .07	16.9± .08	2.90± .09	15.4± .13
Ph139	63	.48± .05	.76± .05	.63± .11	7.98± .28	26.1± .22	18.2± .20	16.0± .22	10.50± .15	78.3± .27	9.8± .12	16.1± .02	3.80± .20	15.1± .15
Ph140	28	.07± .01	.50± .10	.14± .30	9.25± .46	29.4± .52	20.2± .30	14.4± .40	10.00± .25	80.6± .36	10.0± .12	16.2± .04	3.32± .19	15.7± .16
Ph141	54	1.28± .09	1.37± .06	.93± .08	3.67± .37	30.2± .26	26.7± .40	12.9± .23	9.10± .18	78.0± .39	9.8± .14	16.3± .04	3.80± .18	16.0± .21

* 1915 progeny.

DISCUSSION OF RESULTS

The results of the 1916 experiments will first be examined to determine whether they corroborate the 1915 data in showing that there are significant differences among the progenies in the extent of damage.

An examination of the average damage of the different progenies (Table IV, column 2) shows the results to be in fair accord with those of the previous year and shows even more clearly that the differences in the extent of damage are not the result of accident.

Ph124, again the least damaged of all the progenies, is with one exception separated from all other progenies by significant differences. The exception, Ph140, is a descendant of Ph124, produced in 1915, the male parent being a plant of Ph123. From the remaining progenies Ph124 is separated by differences that range from 2.4 to 16.5 times the probable error.

It may be seen also that Oregon Evergreen, P129, one of the commercial varieties included in the experiment, was damaged more than any of the hybrid progenies except Ph127, Ph127C1, and Ph128C2. One of these, Ph127C1, is the only progeny in which the difference is significant. Oregon Evergreen was chosen for comparison as one of the most worm-resistant of the commercial varieties of sweet corn. It is also the variety most generally grown in the worm-infested regions of the Southwest. The relatively high damage in the two Hopi hybrids Ph137 and Ph141 should also be noted. The following notes were taken on an Eastern variety of sweet corn grown by the side of the wormproof corn experiment and maturing at the same time.

Prolongation	2.0±0.2
Number of larvæ	2.4± .1
Damage	3.8± .4
Degree of maturity	8.9± .4

Since the days from silking to harvest were not recorded for the variety, it is not included in Table IV. The degree of maturity was lower than in any of the wormproof progenies, and, since damage is negatively correlated with maturity, the comparison is believed to be in no way unfair. The damage to this variety was nearly 3 times that of the wormproof progeny with the greatest damage, and 29 times that of the progeny least damaged. As a further comparison the average damage to Golden Bantam sweet corn growing in a garden about ¼ mile from the experiment was found to be 2.6 ± 0.5.

Considering only the 14 rows planted from the same lots of seed as the 1915 experiment (marked with an asterisk in Table IV), it will be seen that the row least damaged in 1915 was also the least damaged in 1916. Beyond this, while it can be seen that there is a general agreement, there are many changes in the standing of the progenies. Most of these differences are doubtless to be ascribed to chance variations, for the determinations are by their nature subject to wide fluctuations. It should be kept in mind, however, that the two experiments were tried

in opposite parts of the continent and under widely different environmental conditions. It may well be that the dry, cool climate of the coast of California, where corn is grown under irrigation, would bring into prominence a somewhat different complex of protective factors than the relatively hot, moist climate of Maryland.

Table V gives the general average of the 14 progenies that were planted both seasons with respect to the different characters based on the upper ears and the interannual correlations for the different characters. It will be seen that the infestation was much more severe at Chula Vista, Cal., than at Lanham, Md. This is best indicated by the average number of larvæ. The damage per larva and the total damage were both increased at Chula Vista by the fact that in 1915 many of the ears were allowed to mature before the notes were taken. The pronounced environmental differences between the two localities is indicated by the fact that the time from planting to silking was, on the average, 23 days longer at Chula Vista than at Lanham the following year. In view of the much slower growth of the plants at Chula Vista, it is reasonable to assume that the grains were also slower in maturing. This would expose the ears to the attacks of the larvæ for a longer time and would tend to increase the damage per larva and total damage.

TABLE V.—*General mean of the different characters of 14 progenies in 1915 and 1916 and the interannual correlation*

Factor.	Damage.	Number of larvæ.	Damage per larva.	Prolongation.	Length of husks.	Length of ear.
			Grades.	*Cm.*	*Cm.*	*Cm.*
General mean, 1915	3.22	1.75	1.76	9.32	23.6	14.3
General mean, 1916	.65	.84	.76	5.88	26.6	20.7
Interannual correlation	.37±0.16	.73±0.09	.38±0.16	.79±0.07	.76±0.08	.02±0.19

Factor.	Number of husks.	Number of layers.	Days to silking.	Husk leaves.	Number of rows.
				Grades.	
General mean, 1915	12.9	9.8	105.2	1.55	14.6
General mean, 1916	12.7	9.9	82.0	3.24	15.3
Interannual correlation	.53±0.13	.62±0.11	.51±0.13	.39±0.16	.72±0.09

Seventeen of the progenies grown in 1916 were descended from the fourteen progenies grown in 1915. The behavior of these progenies affords some evidence regarding the intensity of the inheritance of the measured characters. To reduce the agreement between parent and offspring to a quantitative basis, the mean values of the seventeen progenies and the mean values of their parent progenies, both grown in 1916, were correlated. Eight of the new progenies grown in 1916 were not descended from single 1915 progenies, but resulted from crosses between different 1915 progenies. In these cases a midparental value was taken by averaging the mean values of the two parents. The correlation coefficients are given in Table VI.

All of the correlations are positive and all are apparently significant. The average of the coefficients for the 11 measured characters was 0.60.

With such small numbers little confidence can be placed in differences in the correlations found for the different characters. It is interesting, however, that damage and number of larvæ have coefficients as large as those of morphological characters.

TABLE VI.—*Correlations between parents and offspring in corn experiments in 1916*

Damage.	Number of larvæ.	Damage per larva.	Prolongation.	Length of husks.	Length of ear.
0.66±0.09	0.72±0.09	*Grades.* 0.40±0.14	*Cm.* 0.68±0.09	*Cm.* 0.72±0.09	*Cm.* 0.56±0.11
Number of husks.	**Number of layers.**	**Days to silking.**	**Husk leaves.**	**Number of rows.**	**Average.**
0.46±0.13	0.43±0.13	0.61±0.10	*Grades.* 0.53±0.12	0.77±0.12	0.60

MEASURES OF INJURY

Of the characters recorded, three were measures of injury. These are given under the headings "Damage," "Damage per larva," and "Number of larvæ." As might be expected from the nature of the characters, the three measures of injury constitute a closely correlated group. The damage per larva was calculated by dividing the total amount of damage in each progeny by the total number of larvæ. The damage per larva is thus, of course, definitely associated with both damage and number of larvæ. There is, however, a factor in the degree of damage not covered by the two other characters—that is, the number of ears that escape without infestation. These uninfested ears reduce the average damage but do not affect the damage per larva.

Since to lessen the amount of damage is the practical object sought, primary consideration will be given to the relations existing between this character and possible protective characters. The correlations with number of larvæ and damage per larva will be considered only as they may help to elucidate the correlations with damage.

CHARACTERS CORRELATED WITH INJURY

In Table VII are given the interprogeny correlations of the characters measured.

With 31 progenies little significance may be attached to any correlation that is less than 0.35, since to exceed 3 times the probable error the correlation must be at least 0.33. Of the plant characters measured, the following showed a correlation with damage of 0.35 or closer: prolongation, length of husks, number of layers, and days to silking. In addition to these, maturity and husk leaves are significantly correlated with number of larvæ. Among the plant characters the following significant correlations appear: Prolongation with length of husks; length of husks with length of ear; number of husks with number of layers; number of layers with days to silking; days to silking with maturity, days silking to harvest, and husk leaves; maturity with days to harvest and husk leaves.

TABLE VII—*Interprogeny correlations*

Factor.	Damage.	Number of larvæ.	Damage per larva.	Prolongation.	Length of husks.	Length of ear.	Number of husks.	Number of layers.	Days to silking.	Maturity.	Days silking to harvest.	Husk leaves.	Number of rows.
			Grades.	*Cm.*	*Cm.*	*Cm.*				*Grades.*		*Grades.*	
Damage	.....	0.85±0.03	0.88±0.03	−0.71±0.06	−0.68±0.07	0.01±0.12	−0.08±0.12	−0.52±0.09	−0.36±0.10	−0.32±0.11	−0.03±0.12	0.31±0.11	0.05±0.12
Number of larvæ	0.85±0.03	.....	.64± .07	− .60± .08	− .56± .08	.03± .12	− .15± .12	− .51± .09	− .56± .09	− .49± .09	− .25± .12	.52± .09	−.16± .12
Damage per larva	.88± .03	.64± .07	.....	− .75± .05	− .78± .05	.06± .12	− .01± .12	− .45± .10	− .12± .12	− .04± .12	− .12± .12	.12± .12	−.16± .12
Prolongation	−.71± .06	−.60± .08	−.75± .05	.....	.75± .06	−.30± .11	− .10± .12	.25± .12	− .02± .12	− .07± .12	− .04± .12	−.13± .12	.15± .12
Length of husks	−.68± .07	−.56± .08	− 78± .05	.75± .06	.....	.35± .11	− .17± .12	.27± .11	.18± .12	.06± .12	.00± .12	−.08± .12	.15± .12
Length of ear	.01± .12	.03± .12	.06± .12	− .30± .11	.35± .11	.....	.09± .12	.11± .12	.23± .12	.27± .11	.06± .12	.08± .12	.04± .12
Number of husks	−.08± .12	−.15± .12	−.01± .12	− .10± .12	− .17± .12	.09± .12	.....	.68± .07	.05± .12	.04± .12	− .13± .12	−.08± .12	.28± .11
Number of layers	−.52± .09	−.51± .09	−.45± .10	.25± .12	.27± .11	.11± .12	.68± .07	.....	.35± .11	.33± .11	.06± .12	−.30± .11	.33± .11
Days to silking	−.36± .10	−.56± .09	−.12± .12	− .02± .12	.18± .12	.23± .12	.05± .12	.35± .11	.....	.92± .02	.66± .07	−.56± .09	.10± .12
Maturity	−.32± .11	−.49± .09	−.04± .12	− .07± .12	.06± .12	.27± .11	.04± .12	.33± .11	.92± .02	.....	.60± .08	−.35± .11	.02± .12
Days silking to harvest	−.03± .12	−.25± .12	−.12± .12	− .04± .12	.00± .12	.06± .12	− .13± .12	.06± .12	.66± .07	.60± .08	.....	−.21± .12	.22± .12
Husk leaves	.31± .11	.52± .09	.12± .12	− .13± .12	− .08± .12	.08± .12	− .08± .12	− .30± .11	− .56± .09	− .35± .11	− .21± .12	.....	−.08± .12
Number of rows	.05± .12	−.16± .12	−.16± .12	.15± .12	.15± .12	.04± .12	.28± .11	.33± .11	.10± .12	.02± .12	.22± .12	−.08± .12	.....

PROLONGATION OF HUSKS

The distance from the tip of the husks to the tip of the ear—in other words, the distance which the newly hatched larva, if it enters the tip of the husks, must travel before its depredations affect the ear—was first considered. This was the character thought to have been the chief cause of the immunity in the field varieties used as parents.

Of all the characters measured this proved to be the most closely correlated with damage and the number of larvæ, in both instances the correlation being negative. The interprogeny correlation between prolongation and damage was -0.71 ± 0.06 and the regression of damage on prolongation was 1.02—that is, with an average increase of 1 cm. in the prolongation an additional 1 per cent of the crop was saved. The meaning of this regression of 1.02 may be further examined by comparing the damage in the progenies with the greatest and least prolongation. There were 14 progenies whose mean prolongation was less than 5 cm., the average prolongation of this group being 2.9 cm. The average damage in this group of progenies was one grade, or 10 per cent of the total crop. The 12 progenies with the greatest average prolongation, all of which were 6 cm. or over, had an average prolongation of 7.7 cm. and a damage of 0.5 grades, or 5 per cent. Thus, an average increase of 4.8 cm. in prolongation was accompanied by an average reduction of 5 per cent in damage.

The correlation of 0.71 between prolongation and damage is sufficiently close to justify the hope that the method followed is satisfactory and that by increasing the prolongation through hybridization or selection substantial reductions in the damage can be secured. A closer study, however, indicates that the relatively close correlation between prolongation and damage is probably not to be completely explained on the basis of a simple physical protection. The chief reason for doubting the apparent direct relation between prolongation and damage is that prolongation appears to have nearly as much affect on the number of larvæ as on the amount of damage, the correlation being -0.60 ± 0.08. Since all the larvæ found inside the husks were counted, whether they had gained access to the ear or not, prolongation can hardly be held to have reduced the number of larvæ in any such manner as it might be expected to reduce the damage.

If, to gain access to the ear, the larva must eat its way down the silks, prolongation would seem necessarily to be a very effective protection. If, on the other hand, larvæ may force their way between the silks and simply crawl to the ear, prolongation would be much less effective. A very large proportion of the eggs are laid on the silks soon after they appear. The eggs hatch in two or three days and the newly hatched larvæ are only about 1.5 mm. long.[1] From the fact that

[1] QUAINTANCE A. L., and BRUES, C. T. Op. cit.

small larvæ are frequently found among the silks inside the husks with no indication of having eaten their way there, it is inferred that these small worms can crawl down the silks to the tip of the ear. Larvæ hatched on other parts of the plant would on the average be larger when they reach the silks and must eat their way to the ear. Against these larger larvæ a greater prolongation should prove an adequate protection, but they are a comparatively small factor in the total damage, as their depredations are largely confined to the tip of the ear.

In both 1915 and 1916 an attempt was made to record for each ear whether the larvæ entered the ear by traveling down the silks or by eating through the husks. Of the 1,449 earworms found in the damaged ears 1,384 were recorded as having entered from the end and only 65, or 4.5 per cent, by penetrating the husks. The holes so frequently observed in the husks, the presence of which led to the belief that thick, harsh husks would afford protection, are explained as being made by the larvæ when emerging. The few larvæ which gain access to the ear by eating through the husks do not leave a continuous track, for the husks of a young ear are elongating at different rates and the continuity of the hole left by the larva is soon broken.

From the fact that in the compacted silks the larvæ would be close together and the débris left by one larva might conceal other small larvæ, it was thought that there would perhaps be a greater tendency to overlook larvæ in the ears with great prolongation with the result that the number of larvæ in such ears would be underestimated. If errors of this kind were of sufficient magnitude, they might account for the correlation between prolongation and number of larvæ.

As a check against errors in counting the number of larvæ, the percentage of ears that had no larvæ was correlated with prolongation. Whatever may be the difficulties in counting the larvæ, whether an ear contains larvæ or not is a fact easily observed, and in dividing the ears into those with and those without larvæ there would be no tendency to overlook the presence of larvæ in ears with the greater prolongation. The correlation between prolongation and the percentage of ears with larvæ was found to be -0.59, a very close agreement with the -0.60 correlation between number of larvæ and prolongation.

If the relation between prolongation and damage as measured by the interprogeny regression is one of cause and effect—that is, if each increase of a centimeter actually reduces the damage by 1 per cent, the same relation should hold among the individual plants of a progeny. In other words, the intraprogeny regression should be the same as the interprogeny regression. The average intraprogeny correlation of damage and prolongation, which seems the best expression we have for the relations

existing among individuals, is -0.254 ± 0.024 and the intraprogeny regression of damage on prolongation is 0.72.[1]

The apparent effect of prolongation on damage within the progeny is thus found to be only about 70 per cent of the effect indicated by the interprogeny regression.

The closer relation found to exist among the means of the progenies might come about through the interprogeny correlation of prolongation with other protective factors. The general absence of genetic correlations in maize characters would render this explanation improbable, but any explanation of the relation of prolongation to damage should also apply to the relation between prolongation and number of larvæ. It is not clear how prolongation can directly affect the number of larvæ, and the coherence of prolongation with other protective characters is the only explanation that suggests itself. For example, the progenies with the greatest prolongation might be later in maturing. If this were the case and larvæ became less numerous as the season advanced, the closeness of the interprogeny correlation between prolongation and damage would appear to be greater than it really is. To approximate the true effect of prolongation on damage, an attempt must be made to eliminate, as far as possible, the effects of other correlated characters. To do this, resort may be had to "partial correlations."

In the present example the partial correlation between prolongation and damage with respect to days to silking will give, so far as the data permit, the degree of relationship between prolongation and damage

[1] There are many difficulties in the way of securing a satisfactory expression for the intraprogeny correlations of damage and prolongation.

To combine the crude determinations of all the individuals into a single population is to confuse the inter- and intra-progeny correlations. To avoid this it seems better to calculate the intraprogeny correlation for each of the progenies.

There is a further difficulty in the choice of method. The customary product moment method, which is perfectly applicable to the means of the progenies, can not properly be used with the individuals of a single progeny owing to the pronounced skewness of the distribution of damage. In a great many of the progenies approximately one-half of the individuals have zero damage. This division of the plants into two groups, those that were damaged and those that were not, would seem to indicate that the biserial correlation may properly be used.

Differences between the mean prolongation of first and second ears prevent the combining of first and second ears in a single correlation table, but the independent calculation of the coefficient for first and second ears in the separate progenies provides an added check on the reliability of the method.

The method followed has been to calculate the biserial correlation in each of the progenies for both first and second ears. In most of the progenies the division was made between zero damage and a damage of one or more. In a few progenies a more equal division was secured by making the division between palants with a damage of one or less and two or more. No correlation was calculated where the smallest class fell below 10 individuals.

A weighted average of all the coefficients is taken as the best single expression of the intraprogeny correlation.

The mean intraprogeny regression was calculated by the formula. Regression of damage on prolongation=

$$Rdp\frac{\sigma d}{\sigma p}$$

where Rdp=average intraprogeny biserial correlation and σd and σp=the square root of the mean of the weighted squares of the standard deviations.

for constant days to silking—that is, with the differences due to season eliminated.[1]

Damage does become somewhat less as the season advances, $r = -0.36$, but there is also a very slight tendency for the progenies with the longer season to have shorter prolongation, $r = -0.02$. The partial correlation of prolongation and damage for constant days to silking is -0.76. Since the direct correlation is -0.71, the conclusion is that among progenies with the same days to silking the negative correlation between prolongation and damage is, if anything, higher than is indicated by the direct correlation.

The effect of days to silking on the correlations between prolongation and the other measurements of injury are all in the same direction—that is, any effect which days to silking may have had is to make the apparent relationship less close than the true one. The partial correlations for constant days to silking change the direct correlation between prolongation and number of larvæ from -0.60 to -0.73, that between prolongation and damage per larva from -0.75 to -0.76.

In like manner the elimination of difference in "maturity" and "silking to harvest" fails to reduce the correlation between prolongation and the measures of injury. The partial correlation of prolongation and damage for constant maturity raises the direct correlation from -0.71 to -0.79; when constant for "silking to harvest," the direct correlation is unchanged.

Another character that might be suspected of affecting the relation between prolongation and damage is husk leaves. The presence of husk leaves may make the ears either more or less attractive to moths when they are depositing their eggs and thus change the number of larvæ gaining access to the ear.

The partial correlation between prolongation and damage for constant husk leaves indicates that the net result is negligible, since it reduces the direct correlation of -0.71 to only -0.70.

By applying the formula for partial correlations a second, third, and fourth time an expression may be obtained for the correlation between prolongation and damage with season, maturity, "silking to harvest," and husk leaves all constant. This was found to be -0.83. The writers therefore conclude that if the relatively close interprogeny correlation between prolongation and damage is due to the association of prolongation with other protective characters, these characters were not included in the notes.

---

[1] The formula for partial correlations is $r_{12.3} = \frac{r_{12} - (r_{13} r_{23})}{\sqrt{1 - r_{13}^2} \sqrt{1 - r_{23}^2}}$

where r_{12} = correlation between variables 1 and 2,
r_{13} = correlation between variables 1 and 3,
r_{23} = correlation between variables 2 and 3,
and $r_{12.3} = r_{12}$ for constant 3.

The difference between the intra- and inter-progeny regression remains unexplained, and in the light of this disparity it should be kept in mind, no asurance can be given that an increase in the prolongation in other stocks will be followed by the same rapid increase in immunity found in the course of these experiments.

LENGTH OF HUSKS

Length of husks and prolongation are measurements of nearly the same thing. Prolongation, however, may increase in either of two ways. The husks may be longer or the ear may be shorter. The first selections were made for prolongation without special regard to the length of the ear, and it was feared that in so doing there might have been a loss in the length of the ear. Fortunately prolongation is more closely correlated with length of husk than with length of ear. The loss in length of ear has not been material, and the worm-resistant strains have a satisfactory ear length. The average for the different progenies ranges from 15.2 to 26.7 cm. Since little is to be gained by reducing the damage at the expense of the length of ear, it would probably be safer in future work to use length of husks as a basis of selection than to rely on the prolongation.

HUSK LEAVES

The correlation between damage and husk leaves is 0.31. Since husk leaves afford additional surface on which moths can deposit eggs the larvæ of which may gain access to the ear, a positive correlation would be expected. On the other hand, eggs so deposited are to some extent at the expense of eggs which in the absence of husk leaves would be deposited on the silks. Larvæ hatching on the husk leaves would be somewhat delayed in reaching the ear. These larvæ might be expected to do less damage than those hatching on the silks, and for this reason the damage per larva should be negatively correlated with husk leaves.

That the husk leaves do attract the moths or at least afford a location for the eggs is indicated by the positive correlation of husk leaves with number of larvæ, 0.52. The second assumption of an opposite relation with damage per larva does not appear in the direct correlation, which is also positive though only 0.12. It will be shown, however, that in general as the number of larvæ increase the damage per larva also increases, and the partial correlation of husk leaves with damage per larva for constant number of larvæ is, in fact, negative, -0.32. This makes it appear that there is also support for the view that husk leaves tend on the average to reduce the damage done by each larva.

The final results are therefore in accord with the supposition that the manner in which husk leaves increase the damage is through providing additional opportunities for the moth to deposit eggs near the tip of the ear.

Since the reduction in damage per larva is more than outweighed by the increased number of larvæ introduced into the ear, the practical conclusion is that husk leaves are to be avoided in breeding worm-resistant strains.

The regression of damage on husk leaves is 0.98; that is, an increase of one grade in the husk leaves is attended by an increased damage of nearly one grade or about 10 per cent. This relation is not the result of the slight negative correlations between husk leaves and prolongation or length of husks, since the partial correlation between husk leaves and damage for constant prolongation and length of husks is higher than the direct correlations.

NUMBER OF LAYERS AND NUMBER OF HUSKS

Number of layers and number of husks are a closely associated pair of characters, the correlation between them being 0.68.

As a protective character number of layers appears to have the advantage. The direct correlations between number of husks and each of the three measurements of damage are negative, but too low to be of significance; and since the correlations of number of layers with the measures of injury are in every case higher, the correlation between number of husks and damage is doubtless largely a secondary relation, owing to the relatively close relation between husks and layers. The partial correlations between number of husks and the measures of injury for constant number of layers are, in fact, all positive instead of negative.

On the other hand, a large number of layers appears to be a protective character second only to prolongation in importance. The direct correlation between number of layers and damage is -0.52. Its operation must be largely independent of prolongation, for the partial correlation between layers and damage for constant prolongation is -0.51 ± 0.09. With days to silking constant, the correlation is reduced to -0.45 and for both days to silking and prolongation constant the correlation is -0.40.

Since the records show that only 4.5 per cent of the larvæ gained access to ears by penetrating the husks, it is difficult to explain the correlation between number of layers and damage as a result of any direct protection. A large number of layers, which, of course, means wide husks, might bring about a closer wrapping of the husks and thus to some extent impede the progress of the larvæ. It seems more probable, however, that the true relation is that suggested as a partial explanation for the relation between prolongation and damage and that number of layers is positively correlated with some protective character not considered in these experiments.

Since the correlation between layers and number of larvæ is closer than that between layers and damage per larva, a large number of layers

would appear to reduce damage more by reducing the number of larvæ than by reducing the damage per larva, and it is difficult to imagine how a number of layers can have any direct effect on the number of larvæ-unless the idea is entertained that a large number of closely wrapped layers causes the larvæ to desert the ear.

The relation between layers and number of larvæ is not the result of any relation existing between layers and prolongation, since the partial correlation for constant prolongation is −0.47. The interprogeny regression of number of larvæ on layers is 0.12—that is, the number of larvæ is reduced on the average by 0.12 of a larva with the addition of each layer.

The average intraprogeny correlation for these characters is −0.04, and the regression of larvæ on layers is 0.01.

In Table VIII the inter- and intra-progeny standard deviations, correlations, and regressions of the measures of injury and the more important protective characters are brought together for comparison. The uniformly lower values of the intraprogeny regressions as compared with the interprogeny regressions support the idea that there are other import, ant characters not included among those recorded.

TABLE VIII.—*Inter- and intra-progeny standard deviations, correlations, and regressions of the measures of injury and the more important protective characters of corn*

Factor.	Standard deviations.		Correlations.						Regressions.					
			Prolongation.		Number of layers.		Husk leaves.		Prolongation.		Number of layers.		Husk leaves.	
	Interprogeny.	Mean intra-progeny.	Interprogeny.	Mean intra-progeny.	Interprogeny.	Mean intra-progeny.	Interprogeny.	Mean intra-progeny.	Interprogeny.	Mean intra-progeny.	Interprogeny.	Mean intra-progeny.	Interprogeny.	Mean intra-progeny.
Damage.....per cent..	3.74	9.77	−0.71	−0.26	−0.52	−0.10	0.31	0.01	−1.02	−0.72	−1.72	−0.51	0.97	0.05
Number of larvæ.....	.23	.58	− .60	− .13	− .51	− .04	.52	.03	− .54	− .02	− .12	− .01	.10	.01
Prolongation.....cm..	2.58	3.48	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Number of layers.....	1.13	1.90	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Husk leaves.....grades..	1.20	2.01	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

MATURITY

A character often ascribed to sweet varieties is that they remain in an edible condition for a longer time than do field varieties. Comparatively little damage is done after the ears have passed the edible stage, and, if the hardening of the grains was hastened, it seems not unreasonable that the injury should be diminished, and this might be a partial explanation of comparative immunity of field varieties. In the 1916 experiments the majority of the ears were harvested between 16 and

18 days from silking. Correlations involving days to harvest and maturity therefore have relatively little significance. The data are sufficient, however, to prove that differences in the rapidity of maturing could not have been an important factor in causing the differences in damage. In no instance was there a significant interprogeny difference in the average maturity at 16, 17, or 18 days from silking. Neither did the two Hopi hybrids, the table variety of soft corn, and the commercial variety of sweet corn, differ significantly in this respect from the worm-proof progenies. The interprogeny regression of the degree of maturity on days from silking to harvest, of 0.72, indicates that for each additional day that elapses the maturity advances on the average 0.7 of a grade. Since it is almost certain that the regression of maturity on days is not linear, the average difference in maturity between the ears harvested at 16 and at 17 days from silking is perhaps a better criterion of the regressions than that calculated from the correlation coefficients. This difference is 1.3 grades of maturity.

It might have been expected that the progenies requiring the longer season to reach the silking stage would also have required a longer time after silking before reaching the edible condition. This proved not to be the case. The correlation between the degree of maturity and days to silking was positive and close, 0.924. This was to a slight extent due to the fact that silking to harvest averaged slightly longer in the late season progenies, but with silking to harvest constant the partial correlation of maturity and days to silking was 0.88. As a further check on this determination the ratio of "maturity" to "silking to harvest" was correlated with days to silking and found to be 0.73.

Two possible explanations are suggested for this unexpected relation:

(1) The field varieties used as parents in the crosses were longer season than the sweet varieties, and field varieties are supposed to mature the seed more rapidly after fertilization. If there was coherence between these two characteristics, the later maturing parents should mature their seeds more rapidly. It should be recalled, however, that with the same number of days from silking to harvest the writers failed to detect significant difference in the degree of maturity among the different progenies or the nonsweet varieties included in the experiments.

(2) The climatic conditions following the flowering of the later progenies may have been more conducive to rapid maturing of the seeds than earlier in the season. It is difficult to find support for this view in the meteorological conditions of the latter part of the season when the days are shorter and the temperatures no higher. It has often been observed, however, that varieties planted late in the season mature with greater rapidity than the meteorological conditions seem to warrant.

INSTINCTS OF THE MOTHS

That the number of larvæ found in the ears of the different progenies shows significant differences suggests that the moths exercise a choice in depositing their eggs. It is possible to go a step farther and by examining the average amount of damage inflicted by each earworm to determine whether some progenies form a more suitable medium for the larva than others. It would seem that some allowance might have to be made for the crowding of the larvæ and their cannibalistic tendencies, both of which would tend to reduce the damage per larva in ears with a large number of larvæ. It is found, however, that in spite of these factors the correlation between number of larvæ and damage per larva is positive instead of negative—that is, on the average the more larvæ there are in an ear the greater is the damage done by the individual larva. In the light of our present knowledge this would seem to indicate that the instincts of the moth are in accord with the requirements of the larva. In other words, the moth deposits more eggs on the plants most acceptable to the larvæ. The only alternative explanation that suggests itself is that the larvæ desert ears that are distasteful to them.

A further indication that the moths exercise choice in attacking plants is the closeness of the correlation between the extent of damage on first and second ears of the same rows. Since this interprogeny correlation is closer than that between damage and prolongation, the most effective protective character measured, it follows that the close correlation between the damage of first and second ears does not result merely from the fact that both have a similar prolongation.

It might be urged that, since the two ears on a plant frequently come into silk simultaneously, there would be a tendency toward similar infestation. To test this point, the interprogeny correlation between the number of days that elapsed between the silking of first and second ears, and the difference in the number of larvæ found in first and second ears was calculated. The correlation was 0.24 ± 0.10. This correlation, while in the right direction, is too low to explain the similarity of infestation of first and second ears, and may be the result of chance.

If it is correct to assume that a great part of the immunity that has been secured has come about through a correlation between husk characters and some protective character or characters not recorded, it would not be surprising if there were similar correlations between long husks and characters of field varieties that are undesirable in a table corn.

The progenies differed widely in depth of grain and tenderness, but those selected for propagation seem to compare favorably in palatability with their sweet ancestors. Sweet varieties have a larger percentage of sugar than field varieties and the transformation of sugar to starch is

delayed in sweet varieties. It is possible that in these particulars the immune strains might tend to resemble the field parent. So far as has been observed, this has not been the case. Both the percentage of sugar and the retardation of transformation are very difficult to measure accurately, for, in addition to the labor of chemical analysis, the problems are seriously complicated by variations due to the time when the analysis is made and by individual variation. It would seem that, to compare two strains with respect to these characters, it would be necessary to analyze a sufficient number of samples of each variety to secure a reliable average and to repeat this entire process at short intervals, beginning soon after fertilization and continuing until the sugar content was practically constant.

The only evidence obtained on these points is that when gathered at the proper time the immune strains were pronounced by a number of different observers to be fully as sweet as the parent sweet varieties, and that in the regression of maturity on days silking to harvest no consistent differences were found between the immune strains and commercial sweet varieties. That sweet segregates from a cross between sweet and field varieties are not deficient in sugar is shown by the work of Pearl and Bartlett,[1] who found the percentage of sugar in the F_2 segregates of a sweet with dent cross to be higher than in the sweet parent.

CONCLUSIONS

In the southern part of the United States and throughout the Tropics very little sweet corn is grown. The chief reason for this is believed to be the ravages of corn earworm (*Chloridea obsoleta* Fab.).

Attempts to grow sweet varieties in the South usually result in an almost complete destruction of the crop by corn earworms. The native field varieties, on the other hand, escape with relatively slight injury, and are largely used as a substitute for sweet corn.

The most obvious difference between sweet and field varieties that might be expected to affect the activities of the corn earworm is the extent to which the ears are protected by husks. Sweet varieties generally have the husks poorly developed. A possible reason for this may lie in the fact that in the northern part of the Corn Belt one of the most desired characteristics in sweet corn is an early season. Generally speaking, early varieties produce few leaves and few leaves are associated with few husks. There is, therefore, a simple explanation of why commercial varieties of sweet corn have poorly protected ears and the poorly protected ears of sweet varieties afford at least a theory as to why they are especially susceptible to the ravages of the corn earworm.

With these facts in mind the problem was to combine the well-protected character of the ears of southern varieties of field corn with

[1] PEARL, Raymond, and BARTLETT, J. M. MENDELIAN INHERITANCE OF CERTAIN CHEMICAL CHARACTERS IN MAIZE. *In* Ztschr. Indukt. Abstam. u. Vererbungslehre, Bd. 6, Heft 1, 2, p. 1–28, 1 fig. 1911.

the table qualities of sweet varieties in the hope that a sweet variety with some degree of immunity would thus be secured.

Crosses were made between commercial varieties of sweet corn and southern varieties of field corn. Sweet seeds were selected from the first-generation ears, and in the second generation plants with well-covered ears were chosen and propagated. The descendants of these plants have been found to be much less subject to injury from the corn earworm than commercial sweet varieties.

The earworm resistance was tested in 1915 near San Diego, Cal., and in 1916 near Washington, D. C. In both seasons the series of hybrids as a whole was found to be less damaged by the corn earworm than commercial sweet varieties. There were also pronounced differences in the immunity of the progenies derived from the different F_2 generation ears. The close agreement between the extent of damage of first and second ears of the different progenies is taken to indicate that the constitution of the plant is an important factor in the immunity. An effort was made to determine the plant characters which give rise to this comparative immunity.

That the factors concerned in immunity are inherited, and are, thus, capable of improvement is indicated by the correlation between the extent of damage in related progenies. The correlation between the average damage of parent and offspring was 0.66 ± 0.09.

Low damage was found to be significantly correlated with a number of morphological characters. For the most part these morphological characters were also correlated with one another. Of the characters measured, prolongation, or the extent to which the husks exceed the ear, was found to be the most closely correlated with low damage. The interprogeny correlation between prolongation and damage was -0.71, with a regression of 1.02 per cent in damage for each centimeter of prolongation. Within the progenies the average correlation was -0.26 and the regression 0.72. This difference between the inter- and intra-progeny regression is believed to indicate that the protection is in part due to other characters correlated with prolongation and not included in those measured.

The thickness of the covering provided the ear by the husks was also found to be associated with low damage, but since only 5 per cent of the larvæ that reach the ear do so by penetrating the husks here again the relation can hardly be a direct one of cause and effect. From the standpoint of worm resistance husk leaves are also shown to be an undesirable character.

By recording the number of larvæ in each ear it is possible to resolve the total damage into (1) number of larvæ and (2) the average amount of injury done by each larva.

It was found that in the more immune progenies both the number of larvæ and the damage per larva were low. Since the number of larvæ must be determined largely by the choice exercised by the moth in depositing eggs, it follows that the plants avoided by the moths are also the plants which the larvæ find most distasteful. This agreement between the instincts of the adult insect and those of the larva is difficult to explain as the result of morphological characters of the plant and would argue that at least a part of the immunity is the result of chemical differences, perhaps the presence of some volatile substance distasteful alike to the moth and the larva. Both in California and Maryland during the period of the experiments the injury from corn earworms was found to decrease slightly as the season advanced.

From the experiments here reported it appears that by increasing the length and thickness of the husk covering and reducing the husk leaves varieties of sweet corn can be produced in which damage from the corn earworm is materially lessened. No difficulty was experienced in securing by hybridization and selection the desired plant characters in combination with the seed characters of sweet corn.

FLAXWILT: A STUDY OF THE NATURE AND INHERITANCE OF WILT RESISTANCE

By W. H. TISDALE,
Wisconsin Agricultural Experiment Station

INTRODUCTION

The main object of these investigations has been to study the nature and inheritance of wilt resistance. Bolley (*4–11*)[1] has so thoroughly worked out the more practical phases of the problem that it has left a clear field for a study of this kind. It seems important, however, to give, by way of introduction, a few fundamental statements regarding the disease and the causal organism.

The flaxwilt problem has been of great importance in this country and is also a serious problem in some of the flax-growing countries of the East (*5, 12, 19, p. 211–217*). In America the flax industry has been forced rapidly westward, owing to the loss from wilt. The disease is typical of the wilt diseases which are produced by various species of Fusarium. Plants at any age from germination to maturity may be attacked and killed by the parasite. The disease is manifested by a sudden wilting of young seedlings and a yellowing of the foliage of older plants, followed by a wilting which may involve the entire plant or only one side of it, thus causing a bending or twisting of the plant toward the wilted side. The disease is highly destructive to common flax (*Linum usitatissimum*) when grown on thoroughly infected soil, and very often the entire crop is destroyed.

SOURCE OF MATERIAL

Flaxseed and "flax-sick soil" were kindly supplied for this work by Prof. H. L. Bolley,[2] of the North Dakota Agricultural Experiment Station. From plants grown from these seeds in the "sick soil" a species of Fusarium was isolated which agreed in cultural characteristics and pathogenicity with *Fusarium lini* Bolley (*4*). There was a wider range of spore size than Bolley gave in his original description, but this could be accounted for by the difference in environmental conditions under which the spores were produced, as environment was found to

[1] Reference is made by number (italic) to "Literature cited," p. 604–605.

[2] The writer wishes to express his sincere appreciation to Prof. H. L. Bolley for his hearty cooperation in offering invaluable suggestions and in supplying material for the work. He is also indebted to Prof. L. R. Jones, of the Plant Pathology Department, and to Prof. L. J. Cole, of the Experimental Breeding Department, of the University of Wisconsin, for their aid in defining the problems at the outset and for their respective supervision and kindly criticisms of the pathological and breeding phases as they progressed.

have a considerable influence on spore size in pure cultures. This organism, which is no doubt identical with *F. lini*, is the only pathogenic form of Fusarium isolated from flax during this work.

STRAINS OF FLAX USED

In undertaking a study of the inheritance of wilt resistance one of the most important considerations was to obtain for the crosses strains of flax which were highly resistant and strains which were highly susceptible to the disease. A number of both resistant and susceptible strains were obtained from Prof. Bolley. Several varieties of common flax were also obtained from various places in North Dakota and Minnesota. Before the crossing work was begun all of these strains, or varieties, were thoroughly tested as to resistant and susceptible qualities on "flax-sick soil" from North Dakota. Plants for these tests, as well as for all infection experiments, were grown in the greenhouse. Some of the strains proved satisfactory under greenhouse conditions, while others did not. All of the resistant strains except North Dakota Resistant 114 were discarded, that variety being used exclusively, as it proved to be superior in resistance to all other strains tested (Pl. 44, B, *a*). This strain is designated as No. 4 throughout this work. Prof. Bolley in sending the seed of No. 4 says:

> This flax has been growing on the North Dakota State grounds for a number of years and ought to be highly resistant to wilt.

The most satisfactory strain of susceptible flax used is strain 3 (North Dakota Pure-Seed Laboratory No. 14654; Pl. 44, B, *b*). Bolley states that this strain died out completely on his seed plots at the North Dakota station and should be well suited for work of this kind. Two other strains of common flax have been used to some extent, but have not been so satisfactory as No. 3 in giving uniform results. One of these, No. 5—a white-flowered variety(Pl. 45, B, *b*)—was obtained from a linseed mill at Red Wing, Minn. This was the only white-flowered variety tested, and, although it was found to be entirely susceptible, it does not wilt so rapidly and uniformly as No. 3. The other, No. 6 (Pl. 45, A, *d*), is a strain of common flax obtained from Mr. M. S. Kirk, Devils Lake, N. Dak. It is similar to No. 3, but is slightly less susceptible.

DEFINITION OF THE PROBLEM

The first available remedy for controlling flaxwilt was introduced with Bolley's (*4*) discovery of the cause of the disease and his selection of flax plants for wilt resistance. The variation of such disease resistance of individual plants within a variety was the basis for Bolley's selection. This method of selection has likewise been successfully employed in obtaining disease-resistant strains of other cultivated plants (*15*, *18*, *20*, *21*). In connection with this improvement by selection, there has

naturally arisen the question as to the nature of individual variation and the cause of disease resistance. Although there has been considerable theorizing concerning the possible cause, or nature of resistance, very little intensive research has been directed toward a positive solution of the problem. Biffen's (*2*, *3*) hybridization experiments with wheat were the first to throw light on disease resistance as being due to inheritable factors which behave according to the laws of Mendel. It hardly seems possible, however, to explain the inheritance of such a character as resistance on so simple a basis as that stated by Biffen.

Having in mind these questions concerning the nature and inheritance of wilt resistance in flax, the writer undertook the present investigations with the Departments of Plant Pathology and Experimental Breeding at the University of Wisconsin in February, 1915, his objects being (1) to study the mode of penetration of flax plants by *F. lini*, (2) to make comparative studies on the penetration of cabbage seedlings by *F. conglutinans* (3) to determine whether or not *F. lini* enters the resistant flax plant, (4) to study the relation of the fungus to the tissues of susceptible and resistant flax plants, and (5) to study the inheritance of wilt resistance through hybridization. Flax was found to be a most suitable plant for the hybridization work for a number of reasons—namely, it has a short growing season, can be grown to maturity in the greenhouse, is easily cross-pollinated, and highly resistant and susceptible strains are available. Even with these advantages it was not expected that more than a clue as to the nature of the inheritance of wilt resistance might be obtained in the time allotted for the work, since breeding is a slow process and it was necessary to develop methods as the work progressed.

NATURE OF WILT RESISTANCE

MODE OF PENETRATION

Before making a detailed study of the relation of the fungus to the various host tissues it was considered of fundamental importance to know how it enters the host, and to know whether or not it penetrates the resistant plant. There seems to be very little definite information as to the exact mode of entrance of the parasitic soil fungi into their hosts. It was hoped that by using pure-culture methods penetrations of flax and cabbage seedlings by species of Fusarium might be obtained so that they could be detected by aid of the microscope. Bolley (*4*) states that *F. lini* penetrates the young flax plants at any point, through the seed, leaves, stem, or roots. His illustration shows very clearly that the fungus is able to penetrate the cell walls at any point, but he does not show conclusively the initial points of entrance. However, he was dealing with the subject mainly from a practical rather than from a standpoint of detailed microscopical study.

In order to make a careful study of penetration, special culture methods were necessary. Test tubes were prepared by placing in the bottom rolls of filter paper (Pl. 44, A) which were moistened and rendered suitable as a medium for fungus growth by pouring a small amount of melted potato agar over them. These tubes were autoclaved and then planted in equal numbers with seeds of both resistant and susceptible varieties of flax. These seeds had been previously treated for five minutes with a 1-to-1,000 solution of mercuric chlorid. At the time of planting, or in some cases just after the seeds had germinated, some of the tubes containing each strain were innoculated with *F. lini* from a pure culture, while others were left uninoculated to serve as controls, and in most cases these remained free from fungus growth (Pl. 44, A, *b*, *c*). Cabbage seedlings were also grown for penetration studies in tubes prepared as above and inoculated with *F. conglutinans* from a pure culture. The potato agar served as an excellent medium for the growth of the species of Fusarium, which had immediate access to the young seedlings growing in the tubes. As soon as any signs of wilting could be seen, the seedlings were carefully removed from the tubes, mounted on slides in a 20 per cent glycerin solution and examined carefully under the microscope. In this way the root hairs can be easily observed, and almost the entire young root system is so transparent that penetrating hyphæ can be detected. In some cases it was necessary to separate the cortical layer from the inner part of the root tissue in order to be able to examine it closely. This was done by carefully splitting the root on one side with a sharp scalpel and removing the cortical layer, which was then spread on the slide and mounted in glycerin, as mentioned above. Penetration studies were also made with young flax seedlings grown in very loose, infected soil. It is very difficult to obtain clean root hairs from plants grown in soil. The best results were secured by taking the plant up with a large lump of soil which was then dissolved away without destroying all of the root hairs by placing it in a vessel of still water and agitating gently. These roots were then mounted and examined in the same manner as those taken from the tubes. A small amount of eosin placed under the cover slip was often of considerable aid in observing root hairs and hyphæ.

A careful study of slides prepared as above described revealed root-hair (fig. 1, G, H, I), epidermal (fig. 2, 3), and stomatal (fig. 4), penetration of flax seedlings taken from tube cultures; root-hair (fig. 1) and epidermal (fig. 3), penetration of flax seedlings grown in infected soil; and root hair penetration (fig. 1, A, B) of cabbage seedlings taken from tube cultures. The cabbage seedlings produce a more abundant supply of root hairs, and are, for this reason, more desirable for the study of root hair penetration than are flax seedlings. By cross inoculation in tube culture it was found that *Fusarium conglutinans* could penetrate the root hairs of flax seedlings (fig. 1, K). Likewise, *F. lini*

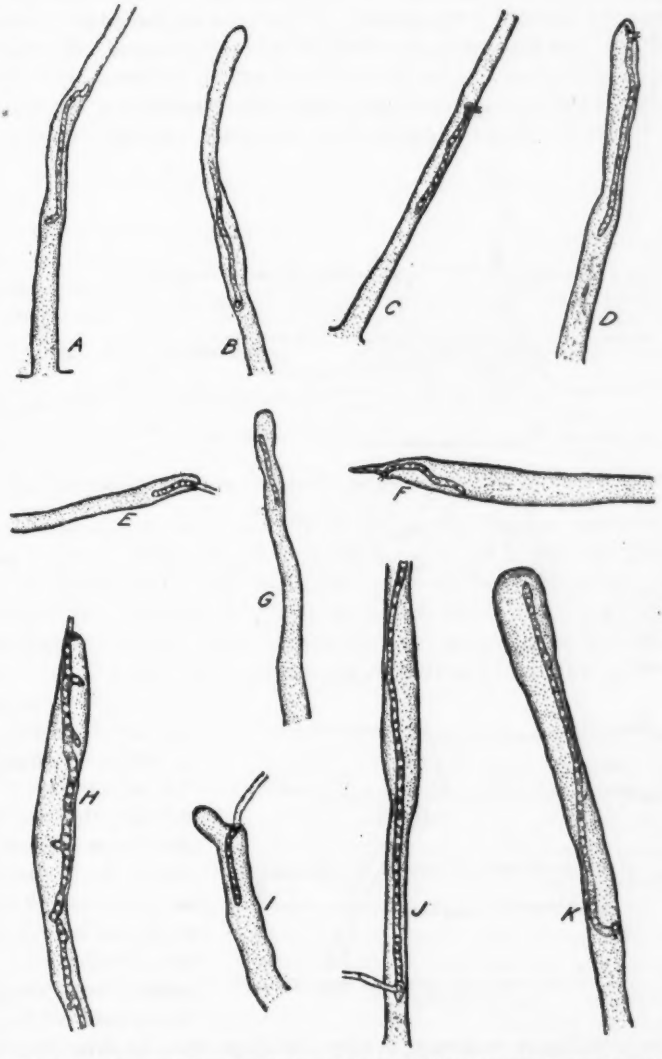


FIG. 1.—A–F, *Fusarium conglutinans* penetrating root hairs of cabbage seedlings in pure culture in test tubes. G, H, and I, *F. lini* penetrating root hairs of flax seedlings grown in test tube cultures. J, *F. lini* penetrating root hair of flax plant grown in loose, infected soil. K, *F. conglutinans* penetrating root hair of flax seedling in pure culture in test tube. Camera-lucida drawings.

was evidently able to penetrate cabbage seedlings as they were killed by it in tube cultures. However, no penetration was observed in the latter as examination was limited. When flax was planted on "cabbage-sick soil" and the reverse, no wilting or yellowing occurred. The fungus, very likely, enters the root hairs to some extent, but probably is unable to invade the tissues of the plant for the same reason that *F. lini* is unable to invade the tissues of the resistant flax plant. It was shown by the

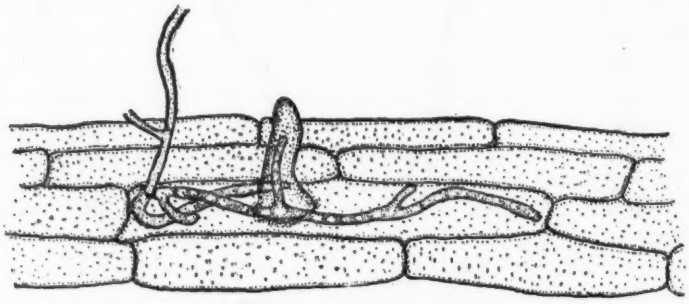


FIG. 2.—*Fusarium lini* penetrating epidermis of young flax root grown in loose, infected soil.

tube-culture method (Pl. 44, A, *a*, *d*) that *F. lini* can penetrate the young seedlings of the resistant strain of flax as readily as it can penetrate the seedlings of the susceptible strain under those conditions.

By what exact means the fungus is able to penetrate the cell walls of the host is not known. Perhaps the most feasible explanation is that given by Ward (*26*) that the fungus protoplasm overcomes the resistance of the cells of the host by means of enzyms or toxins. This might be interpreted as meaning that the fungus secretes an enzym which has a solvent action on the cell wall, or that it may secrete a toxin which prevents any reaction on the part of the host-cell protoplasm by killing or weakening it, thus making possible the invasion of the cell. Perhaps both of these phenomena occur simultaneously. In the case of root-hair penetration there is a slight depression at the point of entrance of the fungus, and the diameter of the opening made by a hypha is somewhat less than the regular diameter of the hypha in question. Stomatal penetration was found on the stem of a young flax seedling near the point where the root began branching. Seedlings taken from the soil

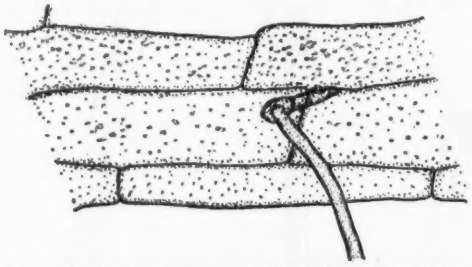


FIG. 3.—*Fusarium lini* penetrating epidermis of young flax seedling in test-tube culture.

showed stomata on the parts which were below the soil surface; therefore it is possible that stomatal penetration is a source of infection as well as root-hair penetration, and the penetration of the epidermis of young roots. The fungus is also capable of infecting through wounds, as was shown by artificial inoculations (Table I). This discovery of root-hair, epidermal, and stomatal penetration bears out Bolley's assumption that the fungus is able to penetrate the young plant at any point.

RELATION OF THE FUNGUS TO THE SUSCEPTIBLE PLANT

The relation of fungi to their host tissues is a very complicated one which varies greatly, according to the fungus and host under consideration. The object of this work was to study the relation of the fungus to the various tissues of the host and to seek any evidence that might be of value in explaining the possible cause for certain disease phenomena.

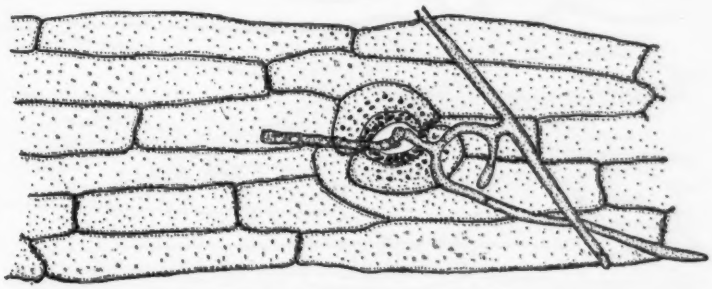


FIG. 4.—*Fusarium lini* entering stoma of young flax seedling in test tube culture.

After entering the susceptible plant, the fungus passes directly through the cell walls of the parenchyma tissues to the vascular system, which it invades to its limits. Bolley (*4*) states that sections through the stems and roots of wilted plants show that the parasite is able to penetrate the cell walls at any point and pass directly through any of the tissues, not excepting the woody parts. This statement holds true especially for plants in the later stages of wilt. Very few fungus hyphæ can be found in the cortical tissues of the stems of plants which have just wilted, although these tissues become thoroughly ramified with hyphæ as the plant begins to decay. The cortical parenchyma of the roots, however, is the first tissue to be invaded by the fungus. In the early stages of the disease the hyphæ are confined largely to the woody tissues in the stem.

Eight newly wilted plants ranging from half-grown to the late-flowering stage were stripped of their foliage, treated for five minutes in a 1-to-1,000 solution of mercuric chlorid, washed in sterile water, cut in pieces with sterile instruments, and plated out on potato agar. Each piece was noted carefully, in order to be sure just what part of the plant it came from. Pure cultures of *F. lini* were obtained from all parts of

the stems of six of these plants up to the terminal bud, and, in one case, growth was obtained from the seed capsules. The two other plants showed growth up to within 1 inch of the terminal bud. Sections taken from near the top of the stem of a plant which had just wilted, and stained with "Pianeze IIIb stain" (*24*) showed the fungus hyphæ in the vascular system but not in the cortex. The method used in staining was varied somewhat from that described by Vaughan (*24*). The slides were passed from xylol through absolute and 95 per cent alcohol into the stain, where they were allowed to remain overnight. They were then washed rapidly in water to remove loose stain and detained in 95 per cent alcohol until the desired point was reached. After detaining they were passed through absolute alcohol and xylol and mounted in balsam

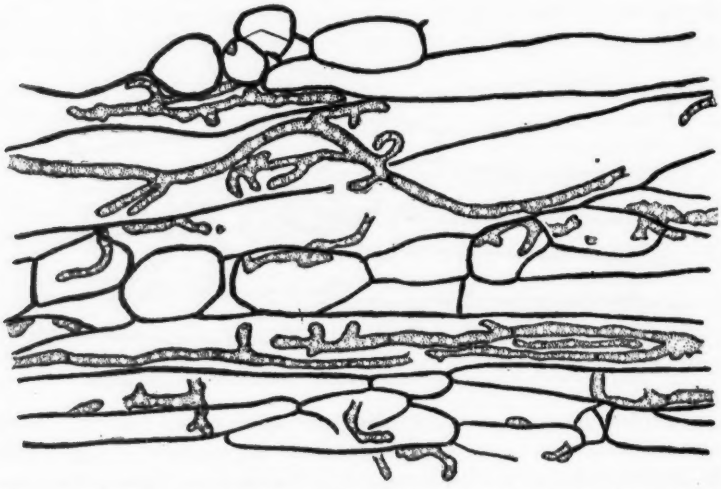


FIG. 5.—Longitudinal section of woody tissues of susceptible flax plant showing the invading hyphæ of *Fusarium lini*.

in the regular manner. Excellent results were obtained by this method of staining.

There seems to be very little reaction on the part of the protoplasm of the susceptible host toward checking the invasion by the fungus. The fungus grows rapidly within the tissues (fig. 5), and sometimes microconidia are produced in the vascular cells of the host plant (fig. 6). Some of the vessels may, in rare cases, become almost clogged with fungus hyphæ (fig. 5), but this is so rare that it would hardly seem possible that the wilting could be due to the cutting off of the water supply by this means (fig. 7). Gilman (*14*) believes that the yellowing of cabbage is due to the slow drain made by *Fusarium conglutinans* on the water supply combined with the high temperature, which causes an increased

growth of the fungus and which increases the transpiration of the plant. This seems reasonable, so far as it goes, but does not seem sufficient for a complete explanation. If it were a case of the water supply being cut off by the clogging of the vessels, we should not expect so much of the one-sided wilting of plants which is so common with flax. The leaves on one side of the stem may become yellow, while those on the other side remain perfectly normal. Stems of plants which are wilted on one side only become characteristically twisted or curved, owing perhaps to unequal growth and shrinkage of tissues. If this wilting were due to the mere cutting off of the water supply at some point, it would be reasonable to except that when a normal plant has its stem cut half-through it would turn yellow and wilt on the cut side. Five flax plants were cut in this way, but none of them showed any yellowing or wilting from the wound. It is certain that by the time the foliage of the plant begins to wilt the root system has been invaded rather severely

FIG. 6.—Longitudinal section of the woody tissue of the susceptible flax plant showing the invading hyphæ of *Fusarium lini*. Notice the microspores of the fungus in the host cells.

by the fungus, and the root hairs are largely destroyed. This is especially true in case of the flax, and would likely account to a considerable extent for any lack in the water supply, and for the general weakening of the plant. Furthermore, there must be a protoplasmic disturbance in cells of the invaded tissues, which helps to produce the local symptoms. Phenonema of this kind might be due to toxic substances produced by the fungus, which interferes with the normal functions of the host protoplasm. The fungus also consumes a part of the food and water supply of the plant. There are very likely, a number of factors which aid in the production of wilt symptoms due to the invasion of flax by *F. lini*—namely (1) Partial destruction of the root system which limits the food and water supply of the plant; (2) use of part of the food and water supply of the plant by the fungus; (3) an increase in transpiration and an increase in the growth of the fungus due to a rise in temperatures; and (4) the possible production of toxic substances by the fungus, which interferes with the normal functions of the host protoplasm.

RELATION OF THE FUNGUS TO THE RESISTANT PLANT

After finding that the fungus was able to penetrate seedlings of the resistant strain of flax in tube cultures, experiments were planned to determine whether or not the fungus was entering the resistant plants growing in infected soil, and, if so, why it was not able to invade the plant and cause wilt. It was found by inoculation experiments that the fungus was unable to produce wilt in resistant plants when introduced through wounds, although infection was obtained by inoculating plants of the susceptible strain. Inoculations were made by inserting bits of mycelium

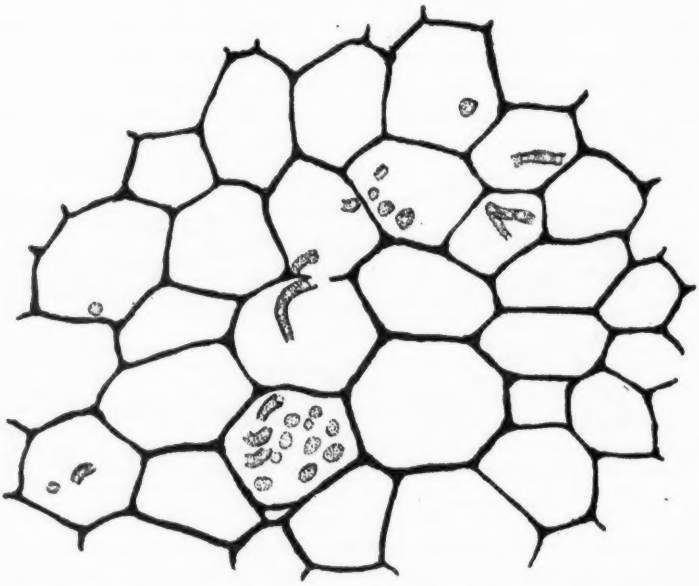


FIG. 7.—Cross section of the vascular tissues of a susceptible flax plant, showing the invading hyphæ of *Fusarium lini*. Camera-lucida drawing.

into needle wounds in the stems of plants. Some were inoculated just above and others just below the soil surface. Stems inoculated above ground were wrapped with moist cotton, while those inoculated below the surface of the ground were covered by replacing the soil. Table I gives the results of these inoculations. It will be seen from this table that the inoculations made in the field were less successful than those made in the greenhouse. The plants in the field were in the flowering stage, which is rather late for infection, and were growing under conditions where the moisture could not be satisfactorily controlled. In the greenhouse young plants were inoculated and kept under better controlled moisture conditions.

TABLE I.—*Results of artificial inoculations of resistant and susceptible flax plants with Fusarium lini*

Date.	Strain of flax.	Number of plants inoculated.	Number of field plants infected.	Number of greenhouse plants infected.
1915.				
August 7	Resistant	7	0	.....
Do	Susceptible	6	0	.....
August 17	Resistant	4	.....	0
Do	Susceptible	2	.....	2
Do	....do	3	.....	3
August 26	Resistant	5	0	.....
Do	Susceptible	5	0	.....
Do	....do	5	0	.....
November 29	Resistant	11	.....	0
Do	Susceptible	1	.....	1
Do	....do	10	.....	3
1916.				
November 26	Resistant	15	.....	0
Do	Susceptible	15	.....	13

Since no infection was obtained by inoculating plants of the resistant strain, while those of the susceptible strain did become infected, it seems that there must be some immediate reaction on the part of the protoplasm of the resistant plant to check invasion by the fungus.

Whatever the nature of resistance, it is not manifested to the highest degree unless the plant is kept under perfectly normal conditions. This fact was shown by the way in which seedlings of the resistant strain of flax were killed by the fungus in tube cultures (Pl. 44, A, *d*), and was further tested by planting disinfected seeds of both the resistant and susceptible strains in flasks of soil which had been sterilized and inoculated with *F. lini*. When these flasks were plugged with cotton and kept in the laboratory, the resistant strain of plants showed slightly more resistance at first, but later succumbed to the attack. However, when flasks were prepared as above and placed in the greenhouse without the cotton plugs, some of the plants of the resistant strain lived to the flowering stage, while plants of the susceptible strain immediately died of wilt. Even under greenhouse conditions, where the temperature runs above normal, some of the plants of the resistant strain wilt.

Careful examination of the root system of resistant plants grown in infected soil showed that some of the smaller roots were decaying and there were brownish spots on the larger roots. A number of these plants which showed no signs of wilt above ground were taken and the root system disinfected thoroughly on the surface with a 1-to-1,000 solution of mercuric chlorid for 2½ to 5 minutes. They were then washed thoroughly and plated out on potato agar. In a large percentage of cases pure cultures of *F. lini* were obtained from these roots. In some cases other

fungi appeared but not in so great an abundance as the parasitic form. Most of the root hairs and very small roots were left in the soil when these plants were removed; therefore the fungus obtained in these experiments came mainly from the larger roots, which were perhaps less likely to be penetrated than the smaller roots. Table II gives the results of these isolation experiments. It will be noticed that roots plated out on February 21, 1916, gave a much lower percentage of *F. lini* than did the others. This is probably due to the fact that these plants were grown in midwinter, when the soil was cooler and the fungus less vigorous. Some of the plants of the resistant strain succumb to the disease in the summer, when the temperatures are high; therefore we should be more likely to find the fungus in the roots under summer conditions, as infection is more abundant.

TABLE II.—*Isolation of Fusarium lini from roots of resistant flax plants*

Date.	Period of treatment with mercuric chlorid.	Number of plant roots plated out.	Number of roots showing growth of *F. lini*.
	Minutes.		
Oct. 4, 1915	2½	3	3
Oct. 7, 1915	2½	7	7
Feb. 21, 1916	5	16	4
Sept. 20, 1916	5	12	12
Sept. 26, 1916	5	28	23

This table shows that the fungus is at least able to penetrate deep enough beneath the surface of the resistant plant to protect it from the mercuric chlorid used in disinfecting the surface, but does not give any evidence as to the extent of invasion.

Parts of the roots of resistant flax plants which showed brown-spotting were fixed in Flemming's medium fixative, embedded, sectioned, and stained with "Pianeze IIIb stain" (*24*) as previously described. This stain gives a pink color with the parenchyma cell walls of the host and with the fungus tissues. With lignified, cutinized, and suberized tissues it gives a light green. A careful study of these sections showed that the fungus entered the parenchyma tissues of the resistant plant (fig. 8), but seldom, if ever, penetrated so far as the xylem elements. This limited invasion by the fungus is accompanied by a number of cellular changes on the part of the host tissues which are in the immediate vicinity of the invading hyphæ.

(1) There is a slight breaking down of the invaded cells which, however, is not sufficient within itself to disconnect the hyphæ from surrounding cells. Marryat (*17*) and Ward (*25*) state that in the case of wheat which resists yellow-rust (caused by *Puccinia glumarum*) there is a sudden breaking down of the first cells to be invaded, thereby cutting

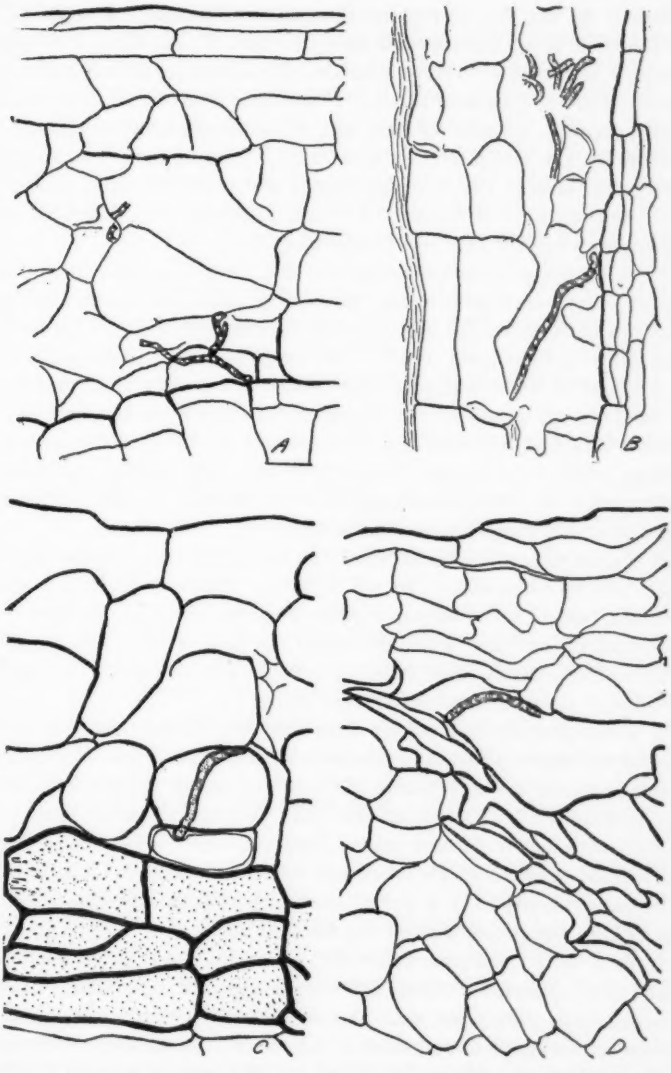


FIG. 8.—A, Longitudinal section of the cortical parenchyma of a resistant flax root showing the formation of cork walls around the point of invasion by *Fusarium lini*. B, Longitudinal section of the cortical parenchyma of a resistant flax root showing a cork layer formed between the point of invasion and the vascular system. Notice the increased cell division beneath the cork layer. C, Longitudinal section of the cortical parenchyma of a resistant flax root showing cell-wall penetration by *F. lini* and the formation of cork walls between the invading hypha and the vascular system of the root. The protoplasm in the cork cells was granular as indicated by stipling. D, Cross section of the cortical parenchyma of a resistant flax root showing the heavy cork walls formed around the point of invasion by *F. lini*. Camera-lucida drawings.

the fungus off from connection with other cells of the host. The fungus then dries up and dies or remains dormant in the dead host cells. The resistant flax plant behaves differently toward *F. lini* than does wheat toward *P. glumarum*. The rust fungus is an obligate parasite and is not capable of growing in dead tissues; *F. lini* may grow either as a parasite or as a saprophyte, and for this reason its development would not be checked by the death of the host cells. Furthermore, the breaking down of the cells in the flax plant is not so complete as that stated for wheat by Marryat and Ward, and would doubtless play very little part in decreasing further invasion by the fungus.

(2) In some cases the protoplasm of the host cells immediately surrounding the point of invasion becomes granular in appearance and stains green with the Pianeze stain, whereas the protoplasm of the normal cell fails to take the green at all. The writer is unable to offer any defiite explanation for this change other than to say that it is possibly a chemical change in the host protoplasm excited by the presence of the fungus. There is doubtless a certain amount of injury to the host protoplasm, which may account in part for the coarse granular condition. Furthermore, as will be mentioned later, there may be some substance produced which is injurious to the fungus.

(3) Surrounding the area in which the cells show the granular appearance, there is a stimulation to cell division. This cell division is more abundant toward the vascular system from the point of invasion. In some cases the dividing walls are formed more or less irregularly, while in other cases a typical cork cambium seems to be formed. The newly-formed cells are to all appearance cork cells.

(4) Accompanying this cell division and other phenomena is a thickening of cell walls, which is much more noticeable toward the vascular system from the invaded point. This thickening of walls may extend three or four cell layers beyond the point of invasion and is more pronounced with newly formed cells. However, the walls of cells which were formed previous to invasion may become thickened. The process of thickening seems to be a laying down of additional material which is produced by the protoplasm of the affected cells. The modification of old walls is more noticeable below and above the point of invasion and toward the epidermis, where cell division is not abundant. These thickened walls stain green with Pianeze stain, which fact indicates that they are either lignified, cutinized, or suberized. In parenchyma tissues of this kind we should hardly expect to find lignin or cutin. When treated with concentrated potassium hydroxid, these walls gave the typical yellow reaction for suberin, which confirms the conclusion that they are of a corky nature.

Taking into consideration the above-mentioned phenomena with other possibilities, it seems that a combined explanation might be offered for the resistance of flax to extensive invasion by *F. lini*. In the first place

the protoplasm of the resistant plant may naturally contain a substance or substances injurious to the fungus. We know that the resistant plant differs from the susceptible plant in respect to its physiological nature. This difference might be due to some permanent chemical composition of the protoplasm as suggested above, or it might possibly be due to a hypersensitiveness of the protoplasm of the resistant plant which causes it to react much more readily than does the protoplasm of the susceptible plant in producing the phenomena which cause resistance. The fungus seems to be less vigorous in the invaded cells of the resistant plant than in the invaded cells of the susceptible plant; in other words, it is less abundant in the cells of the resistant plant. It seems possible, therefore, that some toxic or other chemical substance is produced by the protoplasm of the host which has a deleterious effect on the fungus. The coarse, granular appearance and staining reaction of the protoplasm of the invaded cells indicate that considerable change has taken place. Apparently this change is accompanied by an injury to both the host cells and the fungus hyphæ. Perhaps some substance is produced by the host protoplasm during the change which has an injurious effect on the fungus. When the hyphæ of the fungus come in contact with the modified or corky walls of the cells they fail to penetrate, and further invasion is prevented. Possibly these thickened walls would not be sufficient within themselves to prevent invasion, but they serve as a barrier to the fungus after it has been weakened by protoplasmic reaction on the part of the invaded host cells. These phenomena seem to indicate that resistance is due either directly or indirectly to the chemical nature of the host protoplasm. Appel (*1*) believes resistance in plants to be of a chemical nature and makes the following statement:

> Efforts must be made to find the causes of immunity, and after solving this question to determine without infection the disease-resistant qualities in different varieties and individuals in order to be able to establish the desired resistance and at the same time eliminate undesirable qualities.

Such a theory might at first seem entirely feasible; but, when the multiplicity of constitutional and environmental factors influencing the production of the resistant character is considered, it appears more improbable that any such analysis will ever be satisfactorily made. Ward (*25*, *26*) also speaks of the chemical nature of resistance. He (*26*, p. *21*) says:

> Infection, and resistance to infection, depend on the power of the Fungus-protoplasm to overcome the resistance of the cells of the host by means of enzymes or toxins; and, reciprocally, on that of the protoplasm of the cells of the host to form anti-bodies which destroy such enzymes or toxins, or to excrete chemotactic substances which repel or attack the Fungus-protoplasm.

This theory might be offered as a partial explanation for the resistance of *F. lini* by flax plants.

Finally, if we take into consideration the apparently weakened condition of the fungus in resistant host cells, the change in the nature of the protoplasm of the invaded cells, the new cell division, and the formation of cork walls around the point of invasion, all of which seem to play a part in the prevention of further invasion by the fungus, and all of which are due more or less to the chemical reaction of the host protoplasm, it seems safe to conclude that the resistance of flax to *F. lini* is essentially of a chemical nature.

INHERITANCE OF WILT RESISTANCE THROUGH HYBRIDIZATION

In undertaking a study of the inheritance of wilt resistance though hybridization it was very necessary that highly resistant and susceptible strains of flax be secured and thoroughly tested on infected soil before making crosses. The object of this chapter is to deal with methods of procedure in the work and to give such results as have been obtained from crosses up to date.

METHODS OF SOIL INOCULATION

Before the progeny from crosses could be tested it was highly important that the soil on which the plants were to be grown should be thoroughly infected with the wilt-producing organism, *F. lini*. The soil sent by Prof. Bolley from North Dakota was found by the preliminary tests to be satisfactory (Pl. 44, B), but the quantity was not sufficient. An attempt was therefore made to inoculate soil with pure cultures of the organism. In order to try this out, a small flat of greenhouse soil was sterilized in an autoclave one half being planted to flax No. 3 (susceptible), and the other half to flax No. 4 (resistant). After planting, about half a dozen tube cultures of *F. lini*, which were fruiting abundantly, were mixed thoroughly in a small pot of water and poured over the flat. Wilting of the susceptible plants did not begin until they were of considerable size, but they were completely killed in a short time after the disease started (Pl. 44, C). A large bench of soil was then inoculated. Water suspensions of the organism from pure culture were poured over the soil and worked into the surface. Seeds of the susceptible strain of flax were planted in abundance in the soil. As more fruiting cultures of the organism were obtained, the inoculation was repeated. When the plants from this seed showed considerable wilt they were turned under the soil and more seed planted. Only three or four plantings of this kind were necessary with the pure-culture inoculations to put the soil in suitable condition for the growth of hybrid plants (Pl. 46, A, B). It was also found that from 1½ to 2 inches of the North Dakota soil spread over Madison soil was sufficient to produce thorough wilting of susceptible plants (Pl. 46, C, *b*).

METHODS USED IN CROSSING AND SELFING PLANTS

After thoroughly testing the different strains of flax on "sick soil" and selecting the most suitable ones for the work, crosses were made between plants of the resistant and susceptible strains. The first crosses were made with plants grown in the greenhouse on soil free from *F. lini*. These crosses were fairly successful. In the summer of 1915, plants were grown in the field, and a large number of crosses were made between the different strains in a manner to be described later. These crosses were more successful than those made in the greenhouse. The best results were obtained from crosses made with the first few buds to appear on the plant. This is no doubt due to the fact that the plant is at its maximum sap content and highest state of activity at this stage and is more able to overcome any injury that might be done to the flower through the operation. After the plant becomes more mature, a lower percentage of the artificially pollinated flowers develops. The operation should be performed at about the time when the petals begin to show in the bud. At this stage the authers are not fully mature and are not so easily broken open. The petals can be removed very easily by catching the tip of the bud with a small pair of forceps and pulling gently. Care should be taken not to catch too low on the bud, or the stigma may be broken or injured. Eyre and Smith (*13*) state that they removed the petals by a sudden jerk, removing the stamens at the same time. The writer was not able to do this with the varieties of flax used in this work, without injuring the stigma.

After removing the petals the sepals can be pushed aside and the anthers removed by carefully pinching off the filaments with forceps, which should be sterilized by dipping them in 50 per cent alcohol before and after each operation to avoid contamination. After this operation the flowers are ready for pollination. Flowers pollinated a day after emasculation gave no better results than those pollinated immediately after the process. Pollination is easily accomplished by taking a flower which has just opened from the plant to be used as the male parent and brushing the anthers directly over the stigma of the emasculated flower. It is very easy to tell when the anthers are open by the mealy appearance of the pollen on the surface. Before opening they are smooth and white. After the flower has been pollinated it should be covered to keep out insects and other agents of contamination. Small glacine bags and waxed paper rolled on a fountain pen and tied at the ends were found to be quite satisfactory for protecting the flowers. After the capsules begin to develop it is better to remove the covering, especially in the greenhouse, where there seems to be a smothering of parts covered in this way. In the field, where the rolled paper was used, the seed developed in good condition even though the paper was not removed. The bags, being tighter than the rolled paper, prevented aera-

tion to a greater extent, and for this reason it was more desirable to remove them as soon as possible after the seed began to set.

For selfing plants the paper bags were used very little. The whole plant was covered with cloth. The most satisfactory method was to use wire cylinders about 3 inches in diameter and about 12 inches long, made of screening and covered with slips of finely woven white cloth made to fit. These cloth slips should be considerably longer than the cylinders, so that they can be tied at both ends. A piece of stout wire is pushed into the ground beside the plant, so that it extends a few inches above the top of the plant. The cylinder is then placed over the wire and the plant, and the cloth is brought together at the upper end and tied tightly around the large wire above the top of the plant. The lower end of the cloth is then tied around the wire and the plant above ground. The fruiting part of the plant is thus protected within the cylinder, where it produces seed in a fairly normal manner. These cylinders should be removed as soon as the flowering period is over and the fruit has set.

METHODS USED IN GROWING THE PROGENY FROM CROSSES

Plants of the first and second generations which were to be tested for resistance were grown in flats and on benches of North Dakota "flax-sick soil" and Madison soil which was inoculated as previously stated. These experiments were conducted in the greenhouse throughout the year. There is a slight variation in temperature in the greenhouse with change of seasons, a condition that can not be prevented. It was shown by temperature studies (*23*) that a difference of a few degrees might greatly influence the rate and amount of attack of flax by *F. lini*. By comparing the controls grown in winter and summer this difference will be observable. The high summer temperatures increased the severity of the wilt, even a few plants of the resistant strain wilting.

The soil was well pulverized and the seed planted about 1 inch apart in rows about 4 inches apart. This made it possible to grow a large number of plants in a comparatively small area. In every case rows of both parent strains were planted in every flat or bench in sufficient numbers to serve as controls, and in some experiments selfed seed from the parent plants of the crossed seed were planted as controls. The number of seeds planted was recorded in order to ascertain the percentage of germination. In the summer, when the greenhouse temperature ran high, the percentage of germination was low. In some cases practically none of the seeds germinated. This perhaps was not due to temperature alone but to the increased activity of other physical and biological agents in the soil. As soon as the seed germinated and the seedlings appeared above the ground, they were counted and recorded as plants. Any plant that made its appearance above the ground was counted, even though it died in this stage from wilt. The results are

given with this stage of the plant as a starting point. It would be impossible to determine in every case the exact reason for the failure of the seed to germinate; and as some seeds of both strains did not germinate, it was not thought wise to attribute any of the failure directly to *F. lini*, although it is quite likely that this organism was partly responsible. If there was any doubt as to the cause of the wilting of the seedling after it appeared above the ground, it was determined by isolation methods in the laboratory. After the number of plants was recorded they were kept under almost daily observation. Notes were taken every week where possible and the number of healthy, wilted, and dead plants recorded. Any plant which showed undoubted wilt symptoms was recorded as wilted. This method of note-taking made it possible to compare the rate of wilting of the hybrid plants with that of the susceptible strain. As time and space were very limited it was found to be undesirable to grow all plants to complete maturity. It was then necessary to select some stage in the development of the plant as the end point for observation and note-taking. At this stage all plants which were not to be kept for seed could be removed and other seed planted. The flowering stage was selected as being the most favorable to cease note-taking, for at this stage the plant has reached its maximum activity and very little noticeable infection takes place after this time.

Part of the hybrid seed was grown in clean soil in a different greenhouse where there was no chance for infection by *F. lini*. These plants were self-fertilized as previously described in order to obtain seed for the next generation. By this means seed was obtained from plants that might have been destroyed by wilt if they had been grown in infected soil.

RESULTS OBTAINED FROM THE CROSSES

The parent strains, as previously stated, were thoroughly tested on "flax-sick soil" before the crosses were made and were found to be uniformly resistant or susceptible, as the case might be. However, some of the plants of the resistant strain wilted in later experiments. Results obtained from the progeny of crosses show that there is a great difference in individuality among plants of any strain with respect to its resistance to wilt. This difference was shown very strongly in the two generations grown, the results being so widely different from individual crosses that it will be necessary to discuss the different crosses or groups of crosses separately. The first generation from certain crosses proved to be entirely, or almost entirely, resistant to wilt. Others were intermediate with respect to resistance, while still others were entirely susceptible. In cases where there was entire or partial susceptibility a difference in the time and rate of infection was noticed as compared with the time and rate of infection of the common, susceptible flax. In some experiments the common flax would be almost entirely

dead before the first-generation plants began wilting (Pl. 45, A, B). Later all of these F_1 plants would perhaps succumb to the disease. In some of the experiments there was segregation in the first-generation offspring, part of the plants wilting, while others were as resistant as the resistant parent. In this case there was an intermediate condition as to the time of infection of the F_1 plants also. This fact was apparently not due to excessive vigor of the plants, since vigor seems to play no part in the resistance to wilt by the flax plant. The plants of common flax seem to be even more vigorous than resistant plants in cases, but succumb very readily to the attacks of the fungus.

No such simple ratios were obtained from these flax crosses as Biffen (*2*, *3*) reported from his wheat crosses. Biffen was studying the nature of the inheritance of resistance by wheat to yellow-rust. In his first set of experiments (*2*) he crossed Rivet wheat, which is resistant to yellow-rust, with Michigan Bronze, which he states is probably more susceptible to yellow-rust than any other wheat in existence. The first generation from this cross was entirely susceptible to attacks by the rust. No seed was obtained for a sesond generation, owing to the severity of the attack. Red King, a very susceptible variety, was crossed on Rivet, and the first generation was susceptible in this case also. A second generation from these plants gave practically a 1-to-3 ratio, which Biffen interpreted as indicating that resistance and susceptibility are unit characters, the latter being dominant to the former. Biffen fails to state just where he drew the line between resistance and susceptibility, a very important point. He says the plants which he placed in the resistant group were "relatively" or "almost" free from rust. He also states that the third generation gave results which confirmed those of the preceding generations, but, that statistics for this last generation were not altogether satisfactory, owing partly to the limited amount of grain harvested for the trial and partly to the unfavorable conditions at the time of sowing.

In 1907 Biffen (*3*) published on a piece of work which was much more thorough apparently than his first work. He reported in this case, as before, that the first generation of wheat plants from a cross between entirely immune and susceptible strains was entirely susceptible, and that the second generation gave approximately a ratio of one resistant to three susceptible plants. In these experiments every plant that showed symptoms of rust was considered as susceptible. He also states that there was a gradation between entirely resistant and entirely susceptible plants.

Stuckey (*22*), working with tomatoes at the Georgia Station, states that by crossing the Red Cherry, which is resistant to blossom endrot, with the Greater Baltimore, a large commercial type which is susceptible to the disease, both the first and second generations from the cross were resistant to blossom endrot and that there was no segregation in the second

generation according to Mendelian laws. Unless there is some possibility that these fruits were not subjected to uniformly favorable conditions for blossom endrot, this is apparently an unusual case of inheritance.

Orton (*20, p. 463*) says, in writing on the resistance of farm crops to disease:

> When a disease-resistant variety is crossed with a nonresistant variety, the resulting offspring inherit resistance to a limited and varying extent.

The writer found that in crosses between resistant and susceptible flax plants there was considerable difference in the results obtained from the different progenies. The results seemed to depend largely on the individual plants crossed. One of the most promising crosses made was one between the resistant strain No. 4 and the most susceptible strain, No. 3. The resistant plant was used as female parent, and the progeny was designated as 4D20, "4" referring to the strain, "D" to the plot where the female parent was grown, and "20" to the number of the female plant. With these data on the female parent it was easy to refer to the original records of the cross for the strain of the male parent. This system of recording was used throughout the work. From crosses between the 2 plants mentioned above 5 capsuls were obtained, and 26 first-generation plants were grown on soil thoroughly infected with *F. lini* (Pl. 45, D, *b*). These plants were distributed among three flats, one containing 8 and the two others containing 9 plants each. The plants in one flat were growing at a lower temperature than those in the two other flats, the temperature of the former ranging from 14° to 19° C., while that of the latter ranged from 18° to 21°. None of these F_1 plants, however, were infected, although the controls of susceptible flax No. 3 wilted completely (*23*). They were grown to maturity and seed was obtained for a second generation by selfing. There was a segregation in the second generation into resistant and nonresistant plants. Table III gives the results obtained from the first and second generations and their controls. In this case selfed seed from the parent strains were grown as controls. In order to show the comparison between hybrid plants and plants of the susceptible strain, the number of plants wilted at the end of three weeks and the number killed by wilt at the end of the experiment were recorded.

The second-generation plants, as indicated by the controls given in the table, were grown under somewhat more severe conditions than the first generation, as is shown by the fact that a number of the plants of the resistant parent strain were killed or infected by wilt. The F_1 plants were grown in pure North Dakota soil, while the plants of the second generation were grown in artificially infected soil. Bolley (*9*) says that a change in the type of soil may cause a weakening of the resistant character. There was also a difference of temperature under which these F_1 and F_2 plants were grown, which may have played some part. The F_2 plants were grown in the summer and autumn, while the F_1 plants

were grown in winter and early spring, when the temperature was considerably lower. A slight rise in temperature serves to accelerate the growth of the fungus, and the disease becomes more severe.

TABLE III.—*Resistance to flaxwilt obtained from the progeny of a cross between resistant flax No. 4♀, and susceptible No. 3♂*[a]

Parent strain.	Date of planting.	Number of plants grown.	Ratio at end of three weeks.		Ratio at end of experiment.		Number of plants killed by wilt.
			Wilted.	Not wilted.	Wilted.	Resistant.	
	1916.						
$4D20(F_1)$	Feb. 2	26	0	26	0	26	0
Resistant No. 4	do	39	0	39	0	39	0
Susceptible No. 3	do	52	34	18	52	0	52
F_2 generation:							
4D20–1	July 22	68	37	31	45	23	40
4D20–2	Sept. 23	98	42	56	62	36	53
4D20–3	do	115	40	75	68	47	47
4D20–4	do	28	9	19	22	6	19
4D20–5	do	101	59	42	76	25	64
4D20–6	do	50	29	21	34	16	30
4D20–8	do	70	54	16	61	9	53
Total		530	270	260	368	162	306
Resistant No. 4	Sept. 23	56	6	50	10	46	6
Susceptible No. 3	do	82	76	6	82	0	82

[a] ♀=female; ♂=male.

Since the first generation from this particular cross was entirely resistant, it was hoped that some reasonable explanation might be given for the results obtained in the second generation, although it was apparent at once that they could not be explained on a unit-factor basis. As the number of susceptible F_2 plants was very large, it was thought that they might be explained by Little's (*16*) hypothesis, which is an explanation of cases that appear to be a reversal of dominance. The individuals showing the character in question decrease in number in the F_2 generation, as there is an increase in factors which produce the particular character. The general principle is that with the addition of each factor involved the number of F_2 individuals possessing the character in question is multiplied by 3, while the total number of F_2 individuals is multiplied by 4. The difference between the number of individuals with the character and those lacking it grows progressively greater with each factor added. With the flax cross under consideration, the first generation was entirely resistant to wilt. In the second generation, from a total of 530 plants 162 were resistant and 368 susceptible. These figures approach very closely the expectation, if four factors are concerned in producing resistance. The actual expectation would be 81 resistant to 175 susceptible, which is a ratio of 1 to 2.16. The actual proportion obtained was 81 resistant to 184 susceptible, which is a ratio

of 1 to 2.27. This ratio is fairly close to the expectation. The number of susceptible plants ran rather high, although this was to be expected, since the F_2 plants were grown under slightly abnormal conditions, as we have already seen. Some of these plants showed only slight signs of infection and would no doubt have resisted entirely had they been under less severe conditions. In this case the discrepancy is in the direction expected, the number of susceptible plants running high. Since this is the only cross that gave definite ratios, too much emphasis should not be placed on these results until further experimental evidence is obtained. It is furthermore very desirable that experiments of this kind be conducted in environmental conditions which are kept fairly constant.

TABLE IV.—*Resistance to flaxwilt obtained with reciprocal crosses of resistant flax No. 4 with susceptible No. 3 and their controls*

Parent strain.	Date of planting.	Number of plants grown.	Ratio at end of three weeks.		Ratio at end of experiment.		Number of plants killed by wilt.
			Wilted.	Not wilted.	Wilted.	Resistant.	
	1915.						
4E1 (F_1)	Oct. 15	9	2	7	9	0	9
6E1	do	9	1	8	9	0	9
4E1 (self)	do	17	0	17	0	17	0
6E1 (self)	do	17	13	4	17	0	17
F_2 generation (6E1 ♀ and 4E1 ♂):	1916.						
6E1-1	June 27	76	56	20	67	9	57
6E1-2	do	133	100	33	128	5	115
6E1-3	do	125	56	79	123	2	118
6E1-4	do	104	49	55	101	3	97
6E1-5	do	66	22	44	66	0	65
6E1-6	do	34	15	19	34	0	33
Total		538	298	240	519	19	485
Controls, F_2 generation:							
Resistant No. 4	do	84	12	72	30	54	22
Susceptible No. 6	do	8	8	0	8	0	8
Susceptible No. 3	do	24	24	10	24	0	24
F_2 generation (4E1 ♀, 6E1 ♂):							
4E1-1	do	93	61	32	92	1	84
4E1-2	do	74	52	22	73	1	68
4E1-3	do	36	33	3	36	0	36
4E1-4	do	86	63	23	86	0	84
4E1-5	do	56	31	25	56	0	55
4E1-6	do	84	55	19	80	4	78
Total		429	295	134	423	6	405

Another cross which was followed up with great care was a cross of resistant flax No. 4, with susceptible No. 6. Reciprocal crosses were made, and selfed seed was obtained from both parent plants. The resistant parent is designated as 4E1 and the susceptible parent as 6E1. The first generation (Pl. 45, A, *b*, *c*) proved to be entirely suscept-

ible, although it might be said that there was an intermediate condition, owing to the fact that there was considerable difference in the time of wilting of the first-generation plants as compared with plants grown from selfed seed from the susceptible parent. The second generation was almost entirely susceptible. These plants, however, were grown under more severe conditions than were the plants of the first generation. The severeness of these conditions can be seen from results of the resistant control given in Table IV.

In this case, as is shown by the table, the second-generation plants were grown under fairly severe conditions. Thirty of the eighty-four plants of the resistant control were infected. The second generation was grown on artificially infected soil. Considering the behavior of the first generation and the severe conditions under which the second generation was grown, together with the results obtained, it seems impossible at present to give any direct explanation on a Mendelian basis.

In order to see what the result would be if the seed from the crosses on a number of plants were mixed, seed from five different plants were thrown together and planted. In this case sight was lost of the individuality of parent plants, due to the mixing; consequently, no definite ratios could be expected as individuals behave very differently. Table V gives the results obtained from mixed progeny.

TABLE V.—*Resistance to flaxwilt of the mixed progeny of crosses between resistant flax No. 4♂ and susceptible No. 3♀*

Parent strain.	Date of planting.	Number of plants grown.	Ratio at end of three weeks.		Ratio at end of experiment.		Number of plants killed by wilt.
			Wilted.	Not wilted.	Wilted.	Resistant.	
	1915.						
3E-Mix. (F_1)	Oct. 2	153	53	100	106	47	76
Resistant No. 4	...do....	20	0	20	0	20	0
Susceptible No. 3	...do....	46	43	3	46	0	46
F_2 generation:	1916.						
3E-Mix-1	Apr. 22	89	41	48	49	40	46
3E-Mix-2	...do....	81	63	18	78	3	72
3E-Mix-3	...do....	88	55	33	84	4	67
Total	.....	258	159	99	211	47	185
Resistant No. 4	Apr. 22	45	1	44	[a] 3	42	0
Susceptible No. 3	...do....	43	33	10	43	0	43

[a] Slight.

As is shown by the controls in Table V, these plants were grown under very good conditions for the best test. The resistant parent strains stood up almost perfectly, while every plant of the susceptible parent strain died out completely. Since there are all gradations between an entirely resistant and an entirely susceptible first generation from individual crosses, we would expect the intermediate condition when seed

from a number of individuals are mixed. This was what actually happened. In the second generation there was great variation in the progeny from individuals of this first generation (Pl. 46, B, *c*, *h*). This is what might be expected, since the chances are that each group of second-generation plants came from a different cross. This method of growing the progeny was found to be very unsatisfactory as it gave no direct line on individual crosses which have been found to behave so differently.

TABLE VI.—*Resistance to flaxwilt of the progeny from crosses between resistant and susceptible strains of flax in which about an equal number of resistant and susceptible plants occurred in the first generation*

Parent strain.	Date of planting.	Number of plants grown.	Ratio at end of three weeks.		Ratio at end of experiment.		Number of plants killed by wilt.
			Wilted.	Not wilted.	Wilted.	Resistant.	
RESISTANT NO. 4 ♀ × SUSCEPTIBLE NO. 6 ♂							
	1916						
$4E2$ (F_1)	Apr. 25	6	1	5	3	3	1
Resistant No. 4	...do....	6	0	6	0	6	0
Susceptible No. 6	...do....	9	9	0	9	0	9
F_2 generation:							
$4E2$–1	Sept. 23	26	8	18	15	11	14
$4E2$–2	...do....	37	17	20	24	13	21
Total	.....	63	25	38	39	24	35
Resistant No. 4	Sept. 23	26	4	22	7	19	5
Susceptible No. 3	...do....	24	14	10	24	0	24
RESISTANT NO. 4 ♀ × SUSCEPTIBLE NO. 3 ♂							
	1916						
$4D3$ (F_1)	Feb. 2	18	0	18	10	8	2
Resistant No. 4	...do....	17	0	17	0	17	0
Susceptible No. 3	...do....	16	2	14	16	0	11
F_2 generation:							
$4D3$–1	July 21	74	47	27	73	1	53
$4D3$–2	...do....	63	43	20	61	2	46
$D3$–3	...do....	105	69	36	103	2	82
Total	.....	242	159	83	237	5	181
Resistant No. 4	July 21	37	6	31	14	23	8
Susceptible No. 3	...do....	26	25	1	26	0	26
RESISTANT NO. 4 ♂ AND SUSCEPTIBLE NO. 3 ♀							
	1916						
$3E22$ (F_1)	July 21	9	1	8	4	5	3
Resistant No. 4	...do....	15	0	15	0	15	0
Susceptible No. 3	...do....	18	16	2	18	0	18
F_2 generation:							
$3E22$–2	Sept. 23	24	20	4	23	1	22
Resistant No. 4	...do....	26	4	22	7	19	5
Susceptible No. 3	...do....	24	14	10	24	0	24

A number of cases were discovered in which the first generation split up into almost equal numbers of resistant and susceptible plants, but there seemed to be no definite order of segregation in the second generation in cases of this kind. The severeness of conditions under which these plants were grown can be judged from the controls in each case. Table VI gives results of crosses of this kind.

Another grouping of tables has been made to show the results of crosses where there was a larger number of resistant than susceptible plants in the first generation. There seems to be but little relation between the behavior of the first and second generations from these crosses. Table VII gives the results of crosses of this kind.

TABLE VII.—*Resistance to flaxwilt of crosses between resistant and susceptible strains of flax in which a greater number of resistant than susceptible plants occurred in the first generation*

RESISTANT NO. 4 ♀ × SUSCEPTIBLE NO. 3 ♂

Parent strain.	Date of planting.	Number of plants grown.	Ratio at end of three weeks.		Ratio at end of experiment.		Number of plants killed by wilt.
			Wilted.	Not wilted.	Wilted.	Resistant.	
	1916.						
$4D1(F_1)$	Mar. 29	21	4	17	4	17	2
Resistant No. 4	...do.....	95	5	90	8	87	6
Susceptible No. 3	...do.....	85	80	5	85	0	85
F_2 generation:							
4D1-2	July 22	47	32	15	42	5	36
4D1-3	...do.....	49	41	8	47	2	42
4D1-4	...do.....	41	35	6	37	4	34
4D1-5	...do.....	32	24	8	28	4	24
4D1-6	...do.....	47	35	12	43	4	36
4D1-8	...do.....	49	45	4	47	2	42
Total	...do.....	265	212	53	244	21	214
Resistant No. 4	...do.....	55	12	43	37	18	15
Susceptible No. 3	...do.....	47	45	2	47	0	46

RESISTANT NO. 4 ♂ × SUSCEPTIBLE NO. 5 ♀

$5E1(F)_1$	Feb. 2	8	0	8	2	6	0
Resistant No. 4	...do.....	18	0	18	0	18	0
Susceptible No. 5	...do.....	16	2	14	16	0	16
F_2 generation:							
5E1-1	Sept. 23	78	56	22	67	11	51
5E1-2	...do.....	8	2	6	4	4	4
5E1-3	...do.....	18	8	10	18	0	15
5E1-4	...do.....	24	14	10	21	3	18
5E1-5	...do.....	20	7	13	13	7	10
Total	...do.....	138	87	51	123	25	98
Resistant No. 4	...do.....	26	4	22	7	19	5
Susceptible No. 5	...do.....	2	2	0	2	0	2

TABLE VII.—*Resistance to flaxwilt of crosses between resistant and susceptible strains of flax in which a greater number of resistant than susceptible plants occurred in the first generation*—Continued

RESISTANT NO. 4 ♂ × SUSCEPTIBLE NO. 5 ♀

Parent strain.	Date of planting.	Number of plants grown.	Ratio at end of three weeks.		Ratio at end of experiment.		Number of plants killed by wilt.
			Wilted.	Not wilted.	Wilted.	Resistant.	
	1916.						
$5E22(F_1)$	Apr. 26	14	0	14	5	9	1
Resistant No. 4	...do...	18	0	18	0	18	0
Susceptible No. 5	...do...	16	16	0	16	0	16
F_2 generation:							
$5E22-1$	Sept. 23	53	21	32	40	13	32
Resistant No. 4	...do...	26	4	22	7	19	5
Susceptible No. 5	...do...	2	2	0	2	0	2

RESISTANT NO. 4 ♂ × SUSCEPTIBLE NO. 3 ♀

$3E14(F_1)$	Feb. 2	9	0	9	2	7	0
Resistant No. 4	...do...	14	0	14	0	14	0
Susceptible No. 3	...do...	21	7	14	21	0	21
F_2 generation:							
$3E14-1$	July 21	80	62	18	79	1	67
Resistant No. 4	...do...	26	4	22	7	19	5
Susceptible No. 3	...do...	24	14	10	24	0	24

RESISTANT NO. 4 ♀ × SUSCEPTIBLE NO. 5 ♂

$4E11(F_1)$	Oct. 18	5	0	5	2	3	0
Resistant No. 4	...do...	79	3	76	6	73	3
Susceptible No. 5	...do...	51	36	15	51	0	50
F_2 generation[a]:							
$4E11-1$	...do...	202	55	147	137	65	86
$4E11-2$	...do...	128	63	65	116	12	86
$4E11-3$	...do...	141	30	111	101	40	56
Total	.....	471	148	323	354	117	228

RESISTANT NO. 4 ♀ × SUSCEPTIBLE NO. 5 ♂

$4E7(F_1)$	Oct. 18	5	0	5	2	3	0
Resistant No. 4	...do...	79	3	76	6	73	3
Susceptible No. 5	...do...	51	36	15	51	0	50
F_2 generation[a]:							
$4E7-1$	...do...	44	10	34	18	26	10
$4E7-2$	...do...	52	7	45	16	36	11
Total	.....	96	17	79	34	62	21

[a] Controls for F_2 same as for F_1 above.

Table VIII shows the results of crosses in which the first generation was entirely or almost entirely susceptible. The second generation in these cases behaved about as did the second generation from crosses which have been given above. There seems to be no common explanation for segregation in this case, which, of course, is to be expected when the first generation segregates irregularly, as was true with these crosses.

TABLE VIII.—*Resistance to flax wilt of crosses between resistant and susceptible strains of flax in which the first generation plants were entirely or almost entirely susceptible*

Parent strain.	Date of planting.	Number of plants grown.	Ratio at end of three weeks.		Ratio at end of experiment.		Number of plants killed by wilt.
			Wilted.	Not wilted.	Wilted.	Resistant.	
RESISTANT NO. 4 ♀ × SUSCEPTIBLE NO. 5 ♂							
	1916.						
4E13 (F_1)	Feb. 2	14	4	10	12	2	3
Resistant No. 4	...do....	18	0	18	0	18	0
Susceptible No. 5	...do....	12	6	6	12	0	12
F_2 generation:							
4E13–1	Sept. 23	127	82	45	126	1	125
Resistant No. 4	...do....	26	4	22	7	19	5
Susceptible No. 5	...do....	2	2	0	2	0	2
RESISTANT NO. 4 ♀ × SUSCEPTIBLE NO. 5 ♂							
4E12 (F_1)	Oct. 18	11	5	6	11	0	8
Resistant No. 4	...do....	79	3	76	6	73	3
Susceptible No. 5	...do....	51	36	15	51	0	50
F_2 generation:[a] 4E12–1	...do....	123	62	61	106	17	83

[a] Control same as for F_1.

A large number of first-generation plants have been grown from different crosses from which no second-generation plants have been grown. The first generations from these crosses vary from those which are entirely resistant to those which are entirely susceptible, as have been given in the previous tables. Table IX will show these results.

DISCUSSION OF RESULTS

The inspection of Tables III to IX reveals no common explanation for the results obtained. Except for one case (Table III), no definite ratios could be detected. However, there are a number of possible reasons for these results: (1) The plants were grown under abnormal greenhouse conditions. (2) The temperature was too high in some cases, as previously emphasized. (3) A different type of soil was used for some of the tests, which, according to Bolley (9), is likely to cause a breaking down of the resistant character. (4) There is a great variation among individual plants within a strain.

TABLE IX.—*Resistance to flax wilt of the first generation from individual crosses between resistant and susceptible strains of flax*

Parent strain.	Date of planting.	Number of plants grown.	Ratio at end of three weeks.		Ratio at end of experiment.		Number of plants killed by wilt.
			Wilted.	Not wilted.	Wilted.	Resistant.	
	1916.						
4D30 (F_1)	Feb. 2	18	0	18	0	18	0
4D8 (F_1)	do.	36	0	36	15	21	4
Resistant No. 4	do.	18	0	18	0	18	0
Controls:							
Susceptible No. 3	do.	18	5	13	17	1	13
4D21	Mar. 29	6	1	5	6	0	1
4D38	do.	22	6	16	7	15	3
4D37	do.	32	17	15	32	0	26
4D29	do.	21	16	5	21	0	20
4D26	do.	16	9	7	16	0	12
4D32	do.	17	9	8	17	0	17
4D-mix	do.	88	52	36	82	6	60
Resistant No. 4	do.	95	5	90	8	87	6
Susceptible No. 3	do.	85	80	5	85	0	85
4D36	May 13	16	6	10	6	10	6
4D31	do.	20	9	11	10	10	6
4D23	do.	20	15	5	15	5	11
4D-mix	do.	40	32	8	36	4	26
Resistant No. 4	do.	63	7	56	26	47	4
Susceptible No. 3	do.	75	74	1	75	0	75
6E2	Apr. 25	6	1	5	3	3	1
4E8	do.	8	3	5	4	4	2
5E3	do.	5	4	1	5	0	3
4E6	do.	10	7	3	9	1	4
Resistant No. 4	do.	10	0	10	1	9	0
Susceptible No. 5	do.	5	4	1	5	0	5

However, it seems that there is a possible explanation for the results obtained. The resistant strain of flax has been bred by selection to resist wilt under certain environmental conditions which we might call normal. As was pointed out in Table III, resistance is probably due to a number of factors. Then it might be assumed that under the normal environment certain factors, A, B, C, for example, are required to produce resistance. These factors, which may be of equal or unequal value in producing resistance, are possibly homozygous, as is evidenced by the fact that segregation is exceptional under what is termed a normal environment. If, however, the environment is made more severe, there is a certain amount of segregation among plants of the resistant strain, which was found to be true with plants growing in the greenhouse in the summer. Under these more severe conditions one or more additional factors, D, E, etc., might be supposed to be required to cause the plant to resist. Since the strain has not been selected to resist under these severe conditions of environment, no attempt has been made to make these factors homozygous; therefore they may be absent entirely, or may occur singly or in combination, and may be either homozygous or

heterozygous. Then, a certain amount of segregation would be expected when the plants are subjected to these conditions. Segregation would likewise be expected to take place in the first-generation offspring from crosses of these plants with plants of the susceptible strain, provided the plants are grown in the abnormal environment. Differences of the individual plants of the susceptible strain with regard to the resistant character might account for considerable variation in the amount of segregation in the first generation from such crosses. A difference of this kind has been the basis for the selection of resistant strains. It is possible that some of these plants have one or more of the factors for resistance, which may be either homozygous or heterozygous, but do not have a sufficient number of them to cause the plant to resist where the disease develops normally. In crossing susceptible plants of this kind with plants of the resistant strain various factor combinations would be obtained, some of which would produce resistance in the first generation under the severe conditions while others would not. Results obtained in these experiments could easily be correlated with a theory of this kind.

The perfecting of methods rather than the development of any definite proof of laws governing the inheritance of wilt resistance in flax has been the main accomplishment in this work. Therefore a few helpful suggestions might be offered by way of conclusion of this chapter.

(1) The resistant plant should be tested under severe disease conditions before making the cross. (2) Reciprocal crosses should be made in each case, and selfed seed should be obtained from both parent plants, this to be planted along with the crossed seed. (3) First-generation plants should be grown in disease-free soil to obtain seed for a second generation. (4) First and second-generation plants which are to be tested should be grown under similar conditions with selfed seed from the parents planted as controls. (5) The experiments should be conducted under uniform environmental conditions in order to obtain conclusive results.

CONCLUSIONS

(1) The flax plant is most suitable for a study of the nature and inheritance of wilt resistance, since it grows very well in the greenhouse, has a short growing season, is easily crossed, resistant and susceptible strains are available, and conditions for infection can be produced with certainty.

(2) *Fusarium lini* penetrates the flax plant through root hairs, young epidermal cells, stomata of seedlings, and perhaps through wounds.

(3) *Fusarium conglutinans* is able to penetrate the root hairs of young cabbage seedlings when the seedlings are grown in tube cultures.

(4) *F. lini* invades the various tissues of the susceptible flax plant causing the disease known as flaxwilt. No considerable clogging of

vessels can be seen. Wilting may be due to the combined action of several factors: (a) Destruction of the young active root system by the fungus, which cuts off a part of the food and water supply of the plant. (b) Use of the food and water supply of the plant by the fungus. (c) More vigorous growth of the fungus and increased transpiration of the host plant due to a rise in the temperature. (d) The possible production of toxins by the fungus which injure the host protoplasm.

(5) *F. lini* penetrates the resistant flax plant and stimulates division and cork wall formation in cells adjacent to those attacked, but is not able to invade the tissues to any considerable extent owing to a number of possible reasons: (a) The permanent chemical composition of the resistant plant may be of such nature as to be injurious to the fungus. (b) The protoplasm of the resistant plant may be more highly sensitive than that of the susceptible plant, thus reacting more readily in the production of those phenomena which cause wilt resistance. (3) The stimulation to new cell division and the laying down of cork walls which seem to serve as a barrier to further invasion by the already weakened hyphae.

(6) Wilt resistance in flax is an inheritable character which is apparently determined by multiple factors.

(7) There is a great difference in the individuality of plants of a strain with respect to the resistant character, as shown by their offspring. The first generation from some crosses is entirely resistant, from some intermediate, and from others entirely susceptible.

(8) The degree of resistance shown by a strain of flax depends to a considerable extent on the environmental conditions under which the plants are grown. A strain which was bred to resist under certain conditions may break down under a more severe environment. Plants of North Dakota Resistant No. 114, the best strain employed in this work, was not entirely resistant with the high summer temperatures in the greenhouse.

(9) All parent strains to be used in crossing should be thoroughly tested on infected soil under favorable disease conditions before making the crosses. The resistant parent to be used in the cross should be grown on infected soil.

(10) Hydridization experiments should be conducted under uniform environmental conditions in order to obtain conclusive results. The fact that such varied results were obtained in this work is probably due to the different environments under which the plants were grown.

LITERATURE CITED

(1) APPEL, Otto.
1915. DISEASE RESISTANCE IN PLANTS. *In* Science, n. s., v. 41, no. 1065, p. 773–782.

(2) BIFFEN, R. H.
1905. MENDEL'S LAWS OF INHERITANCE AND WHEAT BREEDING. *In* Jour. Agr. Sci., v. 1, pt. 1, p. 4–48, 2 pl.

(3) ———
1907. STUDIES IN THE INHERITANCE OF DISEASE RESISTANCE. *In* Jour. Agr. Sci., v. 2, pt. 2, p. 109–128.

(4) BOLLEY, H. L.
1901. FLAX WILT AND FLAX-SICK SOIL. N. Dak. Agr. Exp. Sta. Bul. 50, p. 27–58, 16 fig.

(5) ———
1906. FLAX CULTURE. N. Dak. Agr. Exp. Sta. Bul. 71, p. 141–216, 22 pl.

(6) ———
1907. PLANS FOR PROCURING DISEASE RESISTANT CROPS. *In* Proc. Soc. Prom. Agr. Sci., v. 28, p. 107–114.

(7) ———
1908. THE CONSTANCY OF MUTANTS: THE ORIGIN OF DISEASE RESISTANCE IN PLANTS. *In* Amer. Breeders' Assoc. Rpt., v. 4, [1907]/08, p. 121–129.

(8) ———
1908. [REPORT OF THE] DEPARTMENT OF BOTANY. *In* N. Dak. Agr. Exp. Sta., 18th Ann. Rpt., [1907]/08, pt. 1, p. 45–82.

(9) ———
1909. SOME RESULTS AND OBSERVATIONS NOTED IN BREEDING CEREALS IN A SPECIALLY PREPARED DISEASE GARDEN: *In* Amer. Breeders' Assoc. Rpt., v. 5, [1908]/09, p. 177–182.

(10) ———
1911. [REPORT OF THE] DEPARTMENT OF BOTANY. *In* N. Dak. Agr. Exp. Sta., 21st Ann. Rpt., [1910]/11, pt. 1, p. 43–47.

(11) ———
1912. [REPORT OF THE] DEPARTMENT OF BOTANY AND PLANT PATHOLOGY. *In* N. Dak. Agr. Exp. Sta., 22d Ann. Rpt., [1911]/12, pt. 1, p. 23–60.

(12) BROEKEMA, L.
1893. EENIGE WAARNEMINGEN EN DENKBEELDEN OVER DEN VLASBRAND. *In* Landbouwk. Tijdschr., 1893, p. 59–71, 105–128.

(13) EYRE, J. V., and SMITH, G.
1916. SOME NOTES ON THE LINACEAE. THE CROSS POLLINATION OF FLAX. *In* Jour. Genetics, v. 5, no. 3, p. 189–197.

(14) GILMAN, J. C.
1916. CABBAGE YELLOWS AND THE RELATION OF TEMPERATURE TO ITS OCCURENCE. *In* Ann. Mo. Bot. Gard., v. 2, no. 1, p. 25–84, 21 fig., 2 pl. Literature cited, p. 78–81.

(15) JONES, L. R., and GILMAN, J. C.
1915. THE CONTROL OF CABBAGE YELLOWS THROUGH DISEASE RESISTANCE. Wis. Agr. Exp. Sta. Research Bul. 38, 70 p., 23 fig. Literature cited, p. 69–70.

(16) LITTLE, C. C.
1914. A POSSIBLE MENDELIAN EXPLANATION FOR A TYPE OF INHERITANCE APPARENTLY NON-MENDELIAN IN NATURE. *In* Science, n. s., v. 40, no. 1042, p. 904–906.

(17) MARRYAT, Dorothea C. E.
1907. NOTES ON THE INFECTION AND HISTOLOGY OF TWO WHEATS IMMUNE TO THE ATTACKS OF PUCCINIA GLUMARUM, YELLOW RUST. *In* Jour. Agr Sci., v. 2, pt. 2, p. 129–138, 2 pl.

(18) NORTON, J. B.
1913. METHODS USED IN BREEDING ASPARAGUS FOR RUST RESISTANCE. U. S. Dept. Agr. Bur. Plant Indus. Bul. 263, 60 p., 4 fig., 18 pl.

(19) NYPELS, Paul.
1897. NOTES PATHOLOGIQUES. *In* Bul. Soc. Roy. Bot. Belgique, t. 36, pt. 2, p. 183–276, 18 fig.

(20) ORTON, W. A.
1909. THE DEVELOPMENT OF FARM CROPS RESISTANT TO DISEASE. *In* U. S. Dept. Agr. Yearbook, 1908, p. 453–464, pl. 39–40.

(21) ———
1913. THE DEVELOPMENT OF DISEASE RESISTANT VARITIES OF PLANTS. *In* Compt. Rend. 4th Internat. Conf. Génétique, 1911, p. 247–265, 9 fig.

(22) STUCKEY, H. P.
1916. TRANSMISSION OF RESISTANCE AND SUSCEPTIBILITY TO BLOSSOM-END ROT IN TOMATOES. Ga. Agr. Exp. Sta. Bul. 121, p. 83–91, 3 fig.

(23) TISDALE, W. H.
1916. RELATION OF SOIL TEMPERATURE TO INFECTION OF FLAX BY FUSARIUM LINI. *In* Phytopathology, v. 6, no. 5, p. 412–413.

(24) VAUGHAN, R. E.
1914. A METHOD FOR THE DIFFERENTIAL STAINING OF FUNGUS AND HOST CELLS. *In* Ann. Mo. Bot. Gard., v. 1, no. 2, p. 241–242.

(25) WARD, H. M.
1902. ON THE RELATIONS BETWEEN HOST AND PARASITE IN THE BROMES AND THEIR BROWN RUST, PUCCINIA DISPERSA (ERIKSS.). *In* Ann. Bot., v. 16, no. 62, p. 233–315, 3 pl.

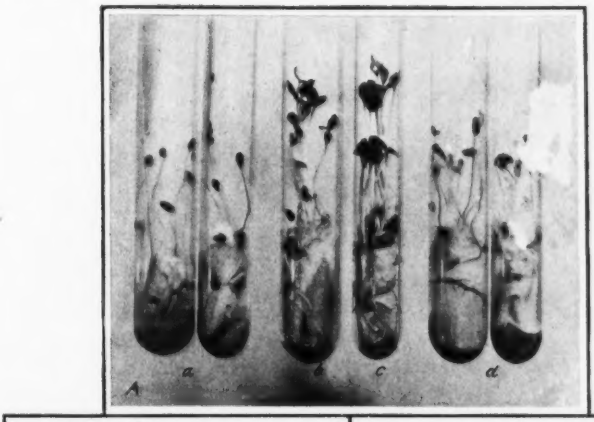
(26) ———
1905. RECENT RESEARCHES ON THE PARASITISM OF FUNGI. *In* Ann. Bot., v. 19, no. 73, p. 1–54. Literature cited, p. 50–54.

PLATE 44

A.—Flax seedlings as grown in the tube culture for penetration studies: *a*, Seedlings of susceptible flax in tubes inoculated with *Fusarium lini*. *b*, Susceptible flax seedlings growing in uninoculated tube. *c*, Resistant flax seedlings growing in uninoculated tube. *d*, Resistant flax seedlings in tubes inoculated with *F. lini*. These seedlings were killed as readily as susceptible seedlings under these conditions.

B.—Flax plants growing in North Dakota "flax-sick soil." *a*, Resistant flax No. 4. *b*, Susceptible No. 3.

C.—Flax plants grown on soil from Madison, Wis. This soil was sterilized and inoculated with pure cultures of *F. lini*. *a*, Susceptible No. 3. *b*, Resistant No. 4.


A
a
b
c
d

B
a
b

C
a
b

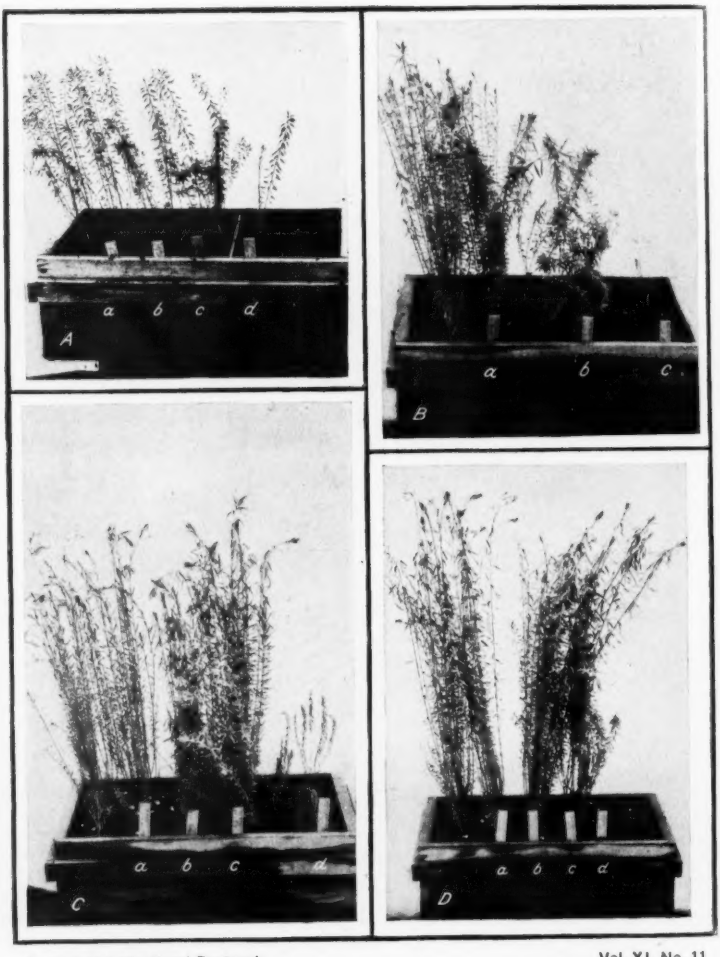

a b c d
A
a b c
B
a b c d
C
a b c d
D

PLATE 45

A.—Flax plants growing on North Dakota "flax-sick soil." *a*, Resistant No. 4. *b*, *c*, Reciprocal crosses between resistant No. 4 and susceptible No. 6. All of these F_1 plants died later of wilt. *d*, Susceptible No. 6.

B.—Flax plants growing in North Dakota "flax-sick soil." *a*, Resistant No. 4. *b*, Cross between resistant No. 4 and susceptible No. 5. *c*, Susceptible No. 5.

C.—Flax plants growing in North Dakota "flax-sick soil." *a*, Resistant No. 4. *b*, *c*, Crosses between resistant No. 4 and susceptible No. 5. *d*, Susceptible No. 5.

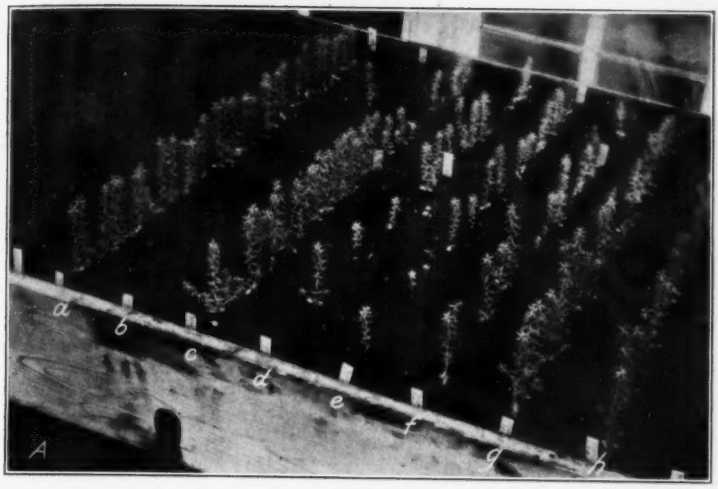
D.—Flax plants growing in North Dakota "flax-sick soil." *a*, Resistant No. 4. *b*, Cross 4D20 between resistant No. 4 and susceptible No. 3. *c*, Cross 3E14 between plants of the same two strains as *b*. *d*, Susceptible No. 3 (all dead).

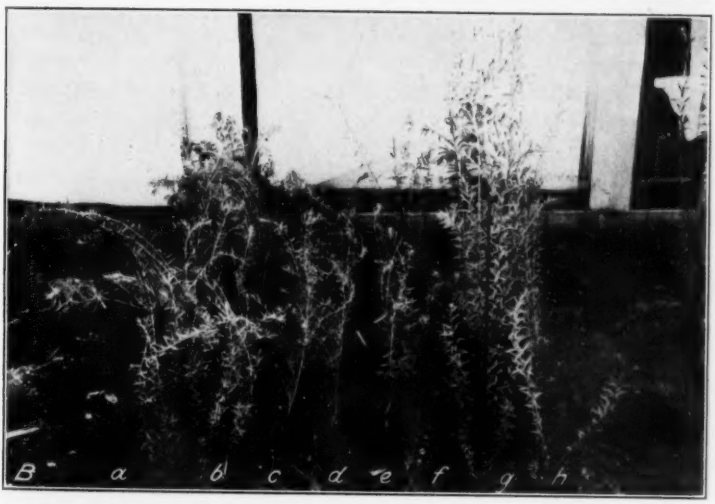
PLATE 46

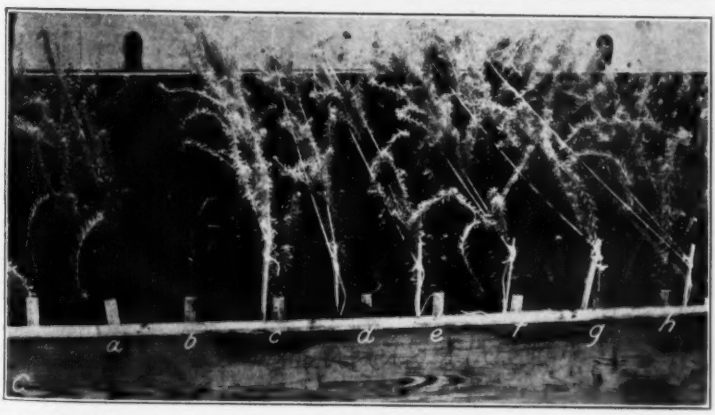
A.—Flax plants growing in soil inoculated artificially with *Fusarium lini*. *a*, Resistant No. 4. *b*, Susceptible No. 3. *c–h*, First-generation plants from crosses between these two strains. Notice that some of the crosses were almost entirely resistant to the disease while others wilted almost as badly as plants of the susceptible strain.

B.—Second-generation flax plants growing on artificially infected soil. *a*, Susceptible No. 3. *b*, Resistant No. 4. *c-h*, Second-generation plants from crosses between these two strains. These plants show the difference in individual plants of the first generation. *c* and *d*, *e* and *f*, *g* and *h*, respectively, came from individual plants of the first generation.

C.—Second-generation flax plants growing in North Dakota "flax-sick soil." *b*, Susceptible No. 3. *c*, Resistant No. 4. *a*, *d-h*, Second-generation plants from the cross 4D20 in which the first generation were all resistant. Of the 530 plants of this F_2 generation 162 were resistant and 368 susceptible.


a
b
c
d
e
f
g
h
A


B
a
b
c
d
e
f
g
h


a
b
c
d
e
f
g
h
C

NATURE AND RATE OF GROWTH IN LAMBS DURING THE FIRST YEAR

By E. G. RITZMAN,[1]

Animal Husbandman, New Hampshire Agricultural Experiment Station

THE PROBLEM

The data presented herewith furnished material for an analysis of the nature and rate of the development of lambs during their first year of growth.

The primary object in view in obtaining these data was the establishment of the normal rate of growth of definite somatic characters for specific periods during this first year of development. The data secured for this purpose, however, were used also in a study of correlation.

In planning this experiment it was decided to take the first record at 2 weeks of age after the lambs had straightened out somewhat, the second at 4 weeks, thereafter monthly up to 3 months of age, and from this time on quarterly up to a year of age. Consequently each lamb was weighed and measured on the dates when it attained these respective periods of age for the first three periods. After the third record was taken, which was at 8 weeks of age, it was found impractical to proceed on this basis, because of the time required to attend to each individual lamb on the date it would attain the age for measurement, so they were divided into groups each of which contained lambs which were within a week of the same age. By taking records of a whole group at one time considerable time was saved. The fourth period covers only 3 weeks instead of 4, as it was found necessary to turn the flock out on pasture at this time when the oldest group of lambs reached the age of 11 weeks. This record was therefore taken before going to pasture, which was one week ahead of the intended schedule because the first week on pasture might result in a temporary reaction to growth owing to the ewes' adjustment to change of feed. The growth periods for which measurements were taken beginning with the second week as shown in Table II are:

1st period	2 weeks	4th period	13 weeks
2d period	4 weeks	5th period	16 weeks
3d period	3 weeks	7th period	12 weeks

[1] Acknowledgment for courteous cooperation is due to members of the Station for Experimental Evolution of the Carnegie Institute, notably to Dr. C. B. Davenport for valuable suggestions and criticism in the preparation of the manuscript and to Dr. J. A. Harris for recalculating and checking the tables of data.

The characters selected for measurement include the following, which it was thought would best serve for the interpretation of size and conformation:

1. Weight (in pounds).
2. Height at shoulder.
3. Head length (sagittal length to horn ridge).
4. Head width (transverse diameter at poll).
5. Neck length (horn ridge to second dorsal vertebra).
6. Trunk length (second dorsal vertebra to tail head).
7. Chest depth (vertical diameter behind foreleg).
8. Chest width (transverse diameter behind foreleg).
9. Loin width (between fourth and fifth lumbar vertebra).
10. Croup length (anterior point of sacrum to tail head).
11. Foreleg length (elbow to ground).
12. Hindleg length (stifle joint to ground).

As nearly all of these measurements of conformation depend on skeletal dimensions, they are not materially influenced by variation in degree of flesh; so that, with the exception of depth and width of chest, the variation in measurements caused by variation in state of flesh is a negligible factor. As the whole flock was maintained under identical conditions of feed and management and was never kept in a high state of flesh, the chest measures give a uniform comparison and vary closely with variations of the skeleton of the chest. Measurements of purely quantitative flesh traits, such as body circumference at chest, neck circumference, and hindleg circumference, were taken but are not included here because they represent condition of flesh rather than size. Body size is determined by the quantitative development of structural characters which are measured as height, length of vertebral axis, depth and spread of frame.

SIZE

Because of a lack of sufficient distinction between size as expressed by weight (which is variable according to condition of flesh) and by structural development (as a framework for carrying flesh) the term when applied to an animal as a whole may become confusing.

Size, in the empirical sense, is expressed in various ways. In meat animals size is commonly expressed by weight; in draft oxen by chest circumference; and in horses by height at withers or weight, or both.

From the geneticists' and breeders' point of view these terms are not only inapplicable, but are often misleading, as no single dimension is adequate to express size.

Structurally, size is expressed in the summation of those dimensions that determine the limits of bulk—dimensions accordingly that are representative of the body type as regards length, depth, and width.

Bulk, or volume, which is probably the best single criterion of size, is here for convenience of comparison measured by the form of two types of

planes:[1] One formed by length with vertical measurements and the other by length with transverse measurements. Length includes four units: (1) Head, (2) neck,[2] (3) trunk, and (4) croup. Height includes four: (1) Total height, (2) chest depth, (3) foreleg length, and (4) hindleg length. These transverse measurements were taken: (1) Head width, (2) chest width, and (3) loin width. The uniformity of the correlations shown in Table III suggests that loin and chest widths reflect either directly or by correlation the relation in variability between length and width.

CONFORMATION

Accepting the length of the vertebral axis as the best linear dimension with which to compare other linear dimensions, we can separate it into three distinct divisions: (1) The head, (2) the neck, and (3) the trunk.

From the economic point of view the first two of these divisions are unimportant, since they contribute no material value to the carcass; nor would any variation in their conformation within normal limits produce any material change in the quantity of fleece.

Conformation is essentially expressed by proportions, in which size as a whole plays no part. It is a term expressing only dimensional relations, of which the ratio of length to breadth and depth are the most important. In a general way conformation may be divided into four types.[3] Assuming that we have four animals of equal trunk length, we may designate these classes as (1) those with relatively deep but narrow bodies; (2) those with relatively broad but shallow bodies; (3) those with bodies that are relatively both deep and broad; and (4) those with bodies that are both shallow and narrow. By these types as a basis we are able to express the general traits of conformation of an animal.

What the specific effect of any variation in ratio of depth to length or of width to length has on the development of two of the major traits (constitution and mutton form) of an animal remains still to be established empirically. Experiments under way here along this line suggest that relative depth of body is the most important if not a perfectly satisfactory index of constitutional development.[4] On the other hand, it is also found that thick flesh, while always associated with relative

[1] These planes are also used to contrast differences in conformation.

[2] Of all dimensions this is the most difficult to obtain with accuracy.

[3] These of course represent extremes between which we find all possible degrees of intermediates.

[4] This is based on the assumption that a chest cavity which is deep in relation to body circumference is associated with relatively larger internal capacity for performing its vital functions and a consequent greater constitutional vigor. In explanation of this point it may be added that cross sections of a number of different types of animals show entirely different results from internal measurements of cross sections than might be expected from external measurements. While external measurements are a good index to internal conditions, they may easily be misinterpreted in animals with a heavy covering of flesh. Furthermore, an animal may be capable of developing a high degree of mutton (with good care and feed) and not possess the desirable degree of constitutional vigor, or the reverse condition may be found as well.

external width,[1] is not necessarily accompanied by a proportional increase in depth. If we view these conditions in relation to length of body, considered in sheep of approximately equal length, we can describe the above classes as (1) strong constitutionally, but of inferior mutton type; (2) good mutton type, but weak constitutionally; (3) strong constitutionally and of good mutton type; and (4) weak constitutionally and of poor mutton type. However, this can be only a generalization applicable within breed types, as there is a marked racial difference in the ratio of depth to width between some breeds, as, for example, the South, down and Rambouillet.

CHANGES THAT OCCUR IN PROPORTIONS DURING GROWTH

In all of our domestic animals the conformation at birth differs more or less from that of the mature state. Young foals, calves, and lambs seem to have disproportionately long legs. In man the reverse is true. Young animals are in many respects undesirably proportioned. While nature exacts these conditions to meet the immediate physiological exigencies attendant on birth, she later makes the correction by differences in the rate and degree of development of different somatic characters; in other words, the growth of the various somatic characters of an animal organism is by no means proportional. These type differences between new-born and adult are shown in Table I. This table shows measurements and weights of 62 animals taken at 14 days of age and again at an average age of 280 days.[2]

Since these measurements are intended to compare conformations rather than to compare size, the 14-day measure has been enlarged, first on the basis of shoulder height at 280 days to contrast comparisons of depth and length, and, second, on the basis of total length [3] to contrast relationship of width and length.

[1] In addition to width (transverse diameter) the hereditary tendency to develop thickness of flesh must also be present.

[2] Only 40 animals are included in the later data, the remainder having been sold or killed by dogs.

[3] Total length is the sum of three other dimensions—head length, neck length, and trunk length.

TABLE I.—*Measurements and weights of 62 sheep when 14 and when 280 days old*

Item.	1	2	3	4	5	6	7
	H × R and Sn × R crosses.	Pure R.	Average at 14 days.	Average at 280 days.	Enlarged scale height.	Enlarged scale length.	Increase.
							Percent.
Number of animals	56	6	62	40	40	40	(a)
Age.....days	14	14	14	280	14	14	.....
Weight.....pounds	15.5	14	15.2	68.7	.....	.....	.....
Height, shoulder.....mm	385	405	390	575	575	640	47.5
Head length.....mm	110	120	115	175	170	185	52.2
Head width.....mm	80	80	80	115	120	130	43.8
Neck length.....mm	175	170	175	285	260	280	62.9
Trunk length.....mm	320	330	320	525	470	520	64.1
Chest depth.....mm	145	135	140	260	205	230	85.7
Chest width.....mm	100	95	100	170	150	165	70.0
Loin width.....mm	75	60	70	120	105	115	71.4
Croup length.....mm	85	75	80	135	120	130	68.8
Foreleg length.....mm	265	280	270	395	400	440	46.3
Hindleg length.....mm	300	315	305	445	450	500	45.9
Ratios:							
Head width / Head length	.....	.....	.....	0.657	0.70	.....	.....
Foreleg length / Trunk length	.....	.....	.....	.753	.846	.....	.....
Chest width / Chest depth	.....	.....	.....	.654	.717	.....	.....
Chest depth / Chest width	.....	.....	.....	.324	.317	.....	.....
Trunk length / Loin width	.....	.....	.....	.229	.221	.....	.....
Trunk length / Croup length	.....	.....	.....	.257	.250	.....	.....
Trunk length / Chest depth	.....	.....	.....	.495	.442	.....	.....
Trunk length / Hind leg length	.....	.....	.....	.404	.962	.....	.....

(a) Column 7 shows the percentage of increase from 14 to 280 days. It is therefore equal to (column 4 — column 3) ÷ column 3.

Columns 5 and 6 of Table I show the average conformation of all lambs measured at exactly 14 days of age[1] and again at an average of 280 days. Owing to losses and sales, the number represented in the older lot is smaller than it was at the beginning.

A comparison of these figures shows the proportions relative to height that exist in conformation at these respective stages of growth. These may be summarized as follows: In developing from 14 to 280 days (comparing columns 5 and 4).

1. The head becomes relatively longer and narrower.
2. The neck becomes relatively longer.
3. The trunk becomes relatively longer.

[1] Measured at 14 days magnified to scale of height at 280 days, column 5, and to scale of length at 280 days column 6.

4. The chest becomes relatively deeper.
5. The chest becomes relatively wider.
6. The loin becomes relatively wider.
7. The croup becomes relatively longer.
8. The leg length remains nearly the same.

In relation to total length of body in developing from 14 days to 280 days (comparing columns 6 and 4).

1. Head narrows and becomes shorter.
2. Neck remains nearly similar in length.
3. Fore and hind legs become much shorter.
4. Chest depth increases.
5. Chest width does not change significantly.
6. Chest depth consequently increases in proportion to chest width.
7. Loin width does not change significantly.
8. Croup length does not change significantly.

These conditions are quantitatively expressed by percentage of increase in column 7. The general deduction is that total height, head width, and leg length increase to about the same relative degree and show least change; chest and loin width, and croup and trunk length show a more marked increase; chest depth increases relatively much more than any other dimension, and that dimensions of width increase relatively slightly in excess of dimensions of length, the latter (length) being similar in neck and trunk but less in the head.[1]

These conditions are further illustrated in figure 1, A–D, in which A and B represent the horizontal plane limited by the total length of vertebral axis and the structurally important transverse dimensions of head width, chest width, and loin width. B represents size and proportions at 280 days, and A, the proportions at 14 days enlarged to equal length of B.

Figure 1, C and D, represents two vertical planes of limits at 14 and 280 days, respectively, where total height, chest depth, leg length, and trunk length are shown in relation to each other. C represents the proportions at 14 days enlarged to equal to the total height of D.

RATE OF GROWTH BY PERIODS

Table II shows measurements and weights by periods for each dimension recorded. A comparison of the quantitative values of dimensions in the upper portion of the table gives a general idea of increase made by each character during each period. The ratios below show some of the changes that occur in the relative proportion between different characters.

[1] The necessity for an unequal rate of development of the various characters becomes obvious when we consider the differences in conformation between the young and the adult stage.

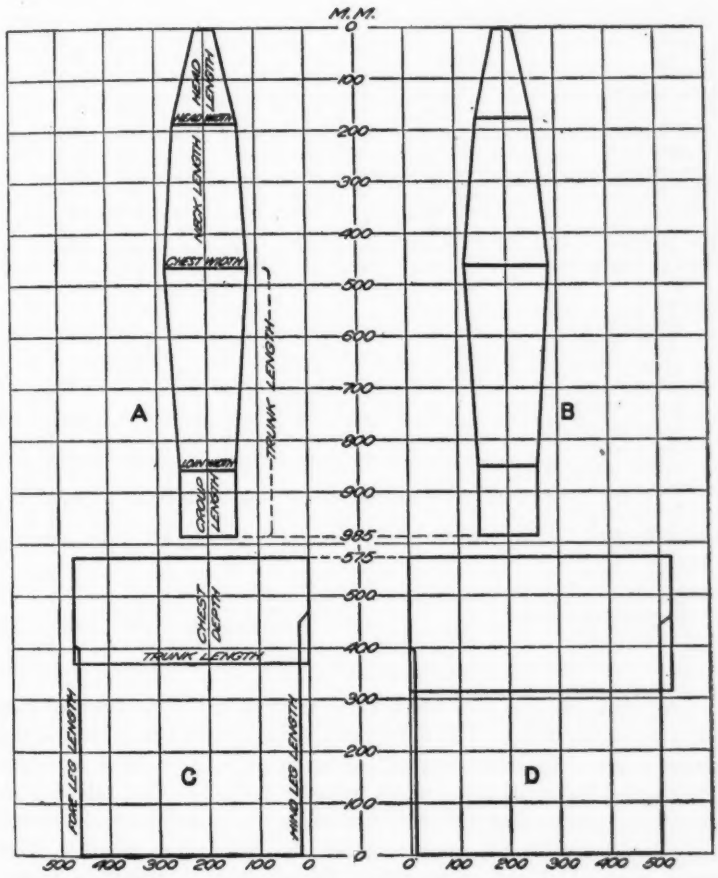


FIG. 1.—Diagrams showing the proportionate growth of lambs at 14 and 280 days: *A*, width of head, chest, and loin when 14 days old; *B*, same when 280 days old; *C*, height, depth of chest, length of legs and trunk when 14 days old; *D*, same when 280 days old.

TABLE II.—*Average measurements and ratios of measurements of lambs by periods (not including pure Rambouillet sheep)*

Item.	Age 2 weeks.	Age 4 weeks.	Age 8 weeks.	Age 12 weeks.	Age 24 weeks.	Age 40 weeks.	Age 52 weeks.
Interval since last measurement, days		14	28	21	91	112	84
Weight.....pounds	15.5	21.5	37.5	450	53.5	660	67
Height.....mm	385	415	475	505	545	575	585
Head length.....mm	110	120	135	145	160	175	185
Head width.....mm	80	85	95	100	105	115	115
Neck length.....mm	175	190	205	220	265	280	280
Trunk length.....mm	320	365	440	475	500	520	540
Chest depth.....mm	145	160	195	210	235	260	265
Chest width.....mm	100	115	130	140	155	170	175
Loin width.....mm	75	80	95	100	110	120	120
Croup length.....mm	85	95	110	120	125	135	135
Foreleg length.....mm	265	280	310	320	360	380	395
Hindleg length.....mm	300	320	360	375	400	435	445
Ratios:							
$\frac{\text{Head width}}{\text{Head length}}$	0.73	0.71	0.70	0.69	0.66	0.66	0.67
$\frac{\text{Chest width}}{\text{Trunk length}}$	.31	.31	.30	.30	.31	.33	.33
$\frac{\text{Loin width}}{\text{Trunk length}}$	.23	.22	.22	.21	.22	.23	.22
$\frac{\text{Croup length}}{\text{Trunk length}}$	.26	.26	.25	.25	.25	.26	.25
$\frac{\text{Foreleg}}{\text{Trunk length}}$	.83	.77	.70	.67	.72	.73	.73
$\frac{\text{Chest depth}}{\text{Trunk length}}$	.45	.44	.44	.44	.47	.50	.49
$\frac{\text{Trunk length}}{\text{Height}}$	.83	.88	.93	.94	.92	.90	.92
$\frac{\text{Chest width}}{\text{Chest depth}}$	.69	.72	.67	.67	.66	.65	.66

The curves in figure 2, of which Table II forms the basis, illustrate this point more forcefully. The most rapid development occurs during the earlier stages of life, decreasing with advancing age, as would be expected. The marked feature of these curves, however, is the fact that, allowing for some variations between different dimensions, they show such an exceedingly rapid growth for approximately the first three months. This period produces at least 50 per cent of the whole year's growth in dimensions and over 60 per cent of the total weight increase for the year under normal care. In the following three months' period there is a considerable decline, probably due in part to two severe temporary checks that occur at this time in this locality, the first occurring when the lambs go out on pasture and the second occurring when they are weaned. Approximately 20 per cent of the whole year's growth is the limit that can be expected for this second quarter. There is about an equal increase in the third quarter which comes during the fall of the year and not over 5 per cent in the last quarter, or winter period.

Economically this is a matter of vital importance in modern methods of sheep husbandry. It emphasizes the fact that under ordinary farm conditions the possibilities of profits are greater when all surplus is sold off at 3 or 4 months of age.[1]

Full structural growth (maturity) is probably attained near the end of the second year under normal conditions. The date must naturally vary somewhat with different breeds, and also with care and environment, as exceptionally favorable conditions of feed, climate, and health accelerate growth, resulting in early maturity with a regular growth curve, whereas

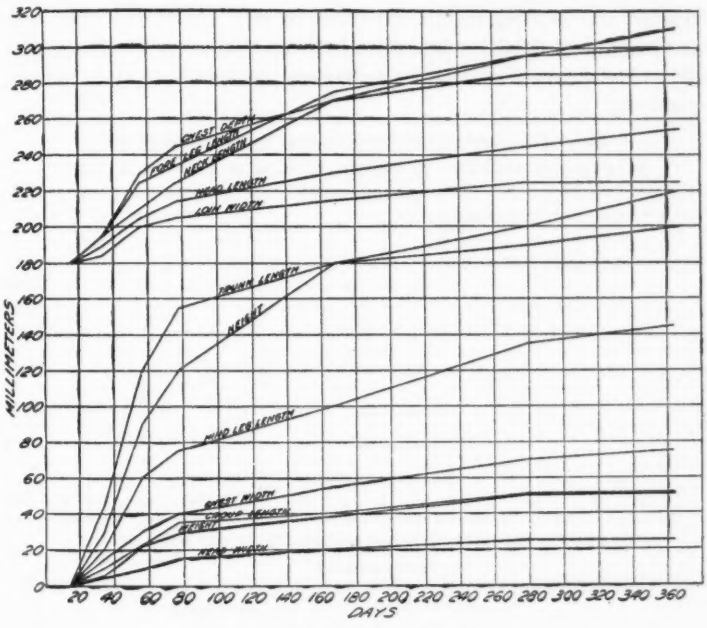


FIG. 2.—Graphs of the development of lambs.

unfavorable conditions of health, feed, and climate, which are incompatible with a normal growth curve earlier in life, may be compensated by growth prolonged beyond the normal time for its logical termination.[2]

If the potential limit of size of these animals is intermediate between the size characters of their adult parentage, then the measurement at 280 days shown indicates that 75 per cent of the total growth has been com-

[1] RITZMAN, E. G. EWES' MILK: ITS FAT CONTENT AND RELATION TO THE GROWTH OF LAMBS. *In* Jour. Agr. Research, v. 8, no. 2, p. 29-36, 1 fig. 1917. Literature cited, p. 35-36.

WATERS, H. J. THE CAPACITY OF ANIMALS TO GROW UNDER ADVERSE CONDITIONS. *In* Proc. 29th Ann. Meeting Soc. Prom. Agr. Sci., 1908, p. 71-96, 5 fig. 1908.

———. THE INFLUENCE OF NUTRITION UPON ANIMAL FORM. *In* Proc. 30th Ann. Meeting Soc. Prom. Agr. Sci., p. 70-98, 6 fig. 1909.

MENDEL, L. B. NUTRITION AND GROWTH. *In* Harvey Lectures delivered under the auspices of the Harvey Society of New York, s. 10, 1914/15, p. 101-131. 1915. Bibliography, p. 128-131.

pleted at this period[1] in all characters except chest width and loin width, which have attained, respectively, only 55 and 65 per cent of their adult state. This exception is quite in accord with general observed facts that widening continues after height or length stature has been completed. All the other curves shown in figure 2 would therefore flatten during the second year even more than during any previous stage, which is quite in harmony with other investigations on growth.

CORRELATION BETWEEN CHARACTERS

Three types of correlations are shown in Table III: (1) Those between characters representing length, (2) those between characters which represent length and depth, and (3) those between characters which represent width. The degree of correlation is shown at the ages of 14 and 280 days, respectively.

TABLE III.—*Correlations between the body measurements of sheep*

HEAD LENGTH RELATIVE TO FORELEG LENGTH AT 14 DAYS OF AGE

[$r=0.443\pm0.068$]

Head length.	Foreleg length.										
	205	215	225	235	245	255	265	275	285	295	Total.
95	....	....	....	....	....	....	....	1	....	....	1
100	....	1	....	....	1	1	....	....	....	....	3
105	2	....	1	1	3	3	5	....	....	....	15
110	....	....	....	1	2	1	5	3	2	....	14
115	....	....	....	....	....	2	....	6	2	1	11
120	....	....	....	....	....	2	4	5	2	....	13
125	....	....	....	....	....	1	....	3	....	....	4
130	....	....	....	....	....	....	....	1	....	....	1
Total	2	1	1	2	6	10	14	19	6	1	62

HEAD LENGTH RELATIVE TO FORELEG LENGTH AT 280 DAYS OF AGE

[$r=0.693\pm0.063$]

Head length.	Foreleg length.									Total.
	355	365	375	385	395	405	415	425	435	
150	1	....	1	....	....	....	....	....	....	2
155	....	....	....	....	....	....	....	....	....	0
160	....	1	1	....	1	....	....	....	....	3
165	....	2	....	....	....	....	....	....	....	2
170	2	3	1	....	....	....	....	....	....	6
175	1	....	5	....	3	1	....	....	....	10
180	....	....	1	3	3	....	2	....	....	9
185	....	....	....	....	1	1	....	....	....	2
190	....	....	....	....	1	....	....	....	....	1
195	....	....	....	....	1	....	....	....	....	1
200	....	....	....	1	....	....	1	....	....	2
205	....	....	....	....	....	....	1	....	1	2
Total	4	6	9	4	10	2	4	0	1	40

[1] This is based on a large number of adult measurements and is quite uniform for all dimensions shown, excepting chest width and loin width.

TABLE III.—*Correlations between the body measurements of sheep*—Continued

HEAD LENGTH RELATIVE TO TRUNK LENGTH AT 14 DAYS OF AGE

[r=0.554±0.059]

Head length.	Trunk length.																
	235	245	255	265	275	285	295	305	315	325	335	345	355	365	375	385	Total.
95	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	1
100	...	...	...	...	...	1	2	...	...	...	...	...	...	...	...	...	3
105	...	...	...	...	1	3	3	5	1	1	1	...	...	...	...	...	15
110	...	1	...	...	1	1	1	2	4	1	2	1	...	...	...	...	14
115	...	...	...	...	...	...	...	...	3	2	3	2	1	...	...	...	11
120	...	...	...	...	...	...	...	2	4	1	5	1	...	...	...	...	13
125	...	...	...	...	...	...	...	...	2	...	1	...	...	...	...	1	4
130	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	1
Total	...	1	...	...	2	5	6	9	14	6	12	4	1	...	1	1	62

HEAD LENGTH RELATIVE TO TRUNK LENGTH AT 280 DAYS OF AGE

[r=0.537±0.076]

Head length.	Trunk length.																
	465	475	485	495	505	515	525	535	545	555	565	575	585	595	605	615	625	Total.
150	...	...	...	...	1	...	1	...	...	...	...	...	...	...	...	...	...	2
155	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0
160	...	...	...	...	1	2	...	...	...	...	...	...	...	...	...	...	...	3
165	...	...	...	...	1	1	...	...	...	...	...	...	...	...	...	...	...	2
170	1	...	...	...	2	1	1	...	1	...	...	...	...	...	...	...	...	6
175	...	1	...	1	2	2	1	3	...	...	...	...	...	...	...	...	...	10
180	...	...	...	1	1	1	1	3	1	1	...	...	...	...	...	...	...	9
185	...	...	...	...	...	...	...	...	1	1	...	...	...	...	...	...	...	2
190	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	1
195	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	1
200	...	...	...	...	1	...	...	...	...	...	...	...	1	...	...	...	...	2
205	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	1	2
Total	1	1	...	2	10	8	4	6	3	2	...	...	2	...	...	...	1	40

FORELEG LENGTH RELATIVE TO TRUNK LENGTH AT 14 DAYS OF AGE

[r=0.498±0.064]

Foreleg length.	Trunk length.															
	245	255	265	275	285	295	305	315	325	335	345	355	365	375	385	Total.
205	...	...	...	2	...	...	...	...	...	...	...	...	...	...	...	2
215	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	1
225	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	1
235	...	...	...	...	1	1	...	...	...	...	...	...	...	...	...	2
245	...	...	...	...	2	2	...	1	...	1	...	...	...	...	...	6
255	...	...	...	...	1	1	1	1	2	3	1	...	...	...	...	10
265	1	...	...	...	...	1	2	5	1	3	1	...	...	...	...	14
275	...	...	...	...	...	...	5	5	2	3	1	1	...	1	1	19
285	...	...	...	...	...	...	1	2	...	2	1	...	...	...	...	6
295	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	1
Total	1	...	...	2	5	6	9	14	6	12	4	1	...	1	1	62

TABLE III.—*Correlations between the body measurements of sheep*—Continued

FORELEG LENGTH RELATIVE TO TRUNK LENGTH AT 280 DAYS OF AGE

[$r=0.700\pm0.054$]

Foreleg length.	Trunk length.																
	465	475	485	495	505	515	525	535	545	555	565	575	585	595	605	615	625	Total.
355	1	1	...	...	...	1	1	...	...	...	...	...	...	...	...	...	...	4
365	...	...	...	...	4	1	1	...	...	...	...	...	...	...	...	...	...	6
375	...	...	...	1	2	2	2	1	1	...	...	...	...	...	...	...	...	9
385	...	...	...	1	2	...	...	...	1	...	...	...	...	...	...	...	...	4
395	...	...	...	...	1	4	...	4	...	1	...	...	...	...	...	...	...	10
405	...	...	...	...	...	...	...	1	1	...	...	...	...	...	...	...	...	2
415	...	...	...	...	1	...	...	...	...	1	...	...	2	...	...	...	...	4
425	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.....
435	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	1
445	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.....
Total	1	1	...	2	10	8	4	6	3	2	...	...	2	...	...	...	1	40

HINDLEG LENGTH RELATIVE TO TRUNK LENGTH AT 14 DAYS OF AGE

[$r=0.557\pm0.074$]

Hindleg length.	Trunk length.																
	235	245	255	265	275	285	295	305	315	325	335	345	355	365	375	385	Total.
235	...	...	...	...	2	...	1	...	1	...	...	...	...	...	...	...	4
245	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0
255	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	1
265	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	1
275	...	...	...	...	...	2	1	...	1	...	...	...	...	...	...	...	4
285	...	...	...	...	...	2	2	1	...	1	1	1	...	...	...	...	8
295	...	1	...	...	...	...	1	2	4	2	3	1	...	...	...	...	14
305	...	...	...	...	...	...	...	3	2	2	1	...	1	...	...	...	9
315	...	...	...	...	...	...	...	2	4	1	7	1	...	...	...	...	15
325	...	...	...	...	...	...	...	...	2	...	...	1	...	...	...	1	4
335	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	1
345	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	1
Total	...	1	...	...	2	5	6	9	14	6	12	4	1	...	1	1	62

TABLE III.—*Correlations between the body measurements of sheep*—Continued

HINDLEG LENGTH RELATIVE TO TRUNK LENGTH AT 280 DAYS OF AGE

[r=0. 474±0.066]

Hindleg length.	Trunk length.																
	465	475	485	495	505	515	525	535	545	555	565	575	585	595	605	615	625	Total.
385	...	...	...	...	...	...	2	...	...	...	...	...	...	...	...	...	...	2
395	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0
405	1	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	2
415	...	1	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	2
425	...	...	...	1	2	2	...	...	...	...	...	...	...	...	...	...	...	5
435	...	...	...	1	2	3	1	3	...	...	...	...	...	...	...	...	...	10
445	...	...	...	...	...	1	1	1	...	1	...	...	1	...	...	...	...	5
455	...	...	...	...	2	2	...	1	1	...	...	...	...	...	...	...	...	6
465	...	...	...	...	2	...	...	...	...	...	...	...	1	...	...	...	...	3
475	...	...	...	...	1	...	...	...	1	...	...	...	...	...	...	...	...	2
485	...	...	...	...	...	...	...	1	...	1	...	...	...	...	...	...	...	2
495	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0
505	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	1
Total	1	1	...	2	10	8	4	6	3	2	...	...	2	...	...	...	1	40

CHEST DEPTH RELATIVE TO TRUNK LENGTH AT 14 DAYS OF AGE

[r=0. 526±0.062]

Chest depth.	Trunk length.																
	235	245	255	265	275	285	295	305	315	325	335	345	355	365	375	385	Total.
100	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0
105	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	1
110	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0
115	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	1
120	...	...	...	...	...	1	...	...	1	...	...	...	...	...	...	...	2
125	...	...	...	...	...	1	3	1	1	...	...	...	...	...	...	...	6
130	...	...	...	...	1	1	1	1	...	...	3	...	...	...	...	...	7
135	...	...	...	...	1	1	...	2	1	...	1	...	...	...	...	...	6
140	...	1	...	...	...	1	...	1	4	2	1	...	...	...	...	...	10
145	...	...	...	...	...	...	1	2	3	1	3	1	...	...	...	...	11
150	...	...	...	...	...	...	...	...	4	2	3	2	1	...	...	...	12
155	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	1	2
160	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	1
165	...	...	...	...	...	...	...	1	...	...	1	...	...	...	1	...	3
Total	...	1	...	...	2	5	6	9	14	6	12	4	1	...	1	1	62

TABLE III.—*Correlations between the body measurements of sheep*—Continued

CHEST DEPTH RELATIVE TO TRUNK LENGTH AT 280 DAYS OF AGE

[r=0.544±0.075]

Chest depth.	Trunk length.																	
	465	475	485	495	505	515	525	535	545	555	565	575	585	595	605	615	625	Total.
225	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	1
230	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0
235	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	1
240	...	...	...	1	2	1	...	...	...	...	...	...	...	...	...	...	...	4
245	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	1
250	...	1	...	...	3	1	...	1	...	...	...	...	...	...	...	...	...	6
255	1	...	...	...	...	2	1	1	...	...	...	...	...	...	...	...	...	5
260	...	...	...	1	1	1	1	2	...	...	...	...	...	...	...	...	...	6
265	...	...	...	...	...	2	1	...	1	1	...	...	...	...	...	...	...	5
270	...	...	...	...	1	...	...	...	1	...	...	...	...	...	...	...	1	3
275	...	...	...	...	...	...	...	2	...	1	...	...	...	...	...	...	...	3
280	...	...	...	...	1	...	...	...	1	...	...	...	...	...	...	...	...	2
285	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	1
290	...	...	...	...	...	...	...	...	...	...	...	...	2	...	...	...	...	2
Total	1	1	...	2	10	8	4	6	3	2	...	...	2	...	...	...	1	40

HEIGHT RELATIVE TO TRUNK LENGTH AT 14 DAYS OF AGE

[r=0.564±0.058]

Height.	Trunk length.																
	235	245	255	265	275	285	295	305	315	325	335	345	355	365	375	385	Total.
335	...	...	...	...	...	...	2	...	...	...	...	...	...	...	...	...	2
345	...	...	...	...	...	2	...	1	...	1	1	...	...	...	...	...	5
355	...	...	...	...	...	...	2	...	2	...	...	...	...	...	...	...	4
365	...	...	...	...	...	2	2	1	1	...	...	...	...	...	...	...	6
375	...	1	...	...	2	...	...	...	2	2	2	...	...	...	...	...	9
385	...	...	...	...	...	1	...	2	1	1	1	1	...	...	...	...	7
395	...	...	...	...	...	...	...	2	3	...	3	2	...	...	...	...	10
405	...	...	...	...	...	...	...	2	3	1	1	...	...	...	...	...	7
415	...	...	...	...	...	...	...	1	2	...	2	1	...	...	...	...	6
425	...	...	...	...	...	...	...	...	...	...	2	...	1	...	...	...	3
435	...	...	...	...	...	...	...	...	...	1	...	...	...	...	1	...	2
445	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	1
Total	...	1	...	...	2	5	6	9	14	6	12	4	1	...	1	1	62

TABLE III.—*Correlations between the body measurements of sheep*—Continued

HEIGHT RELATIVE TO TRUNK LENGTH AT 280 DAYS OF AGE

[r=0.609±0.067]

Height.	Trunk length.																	
	465	475	485	495	505	515	525	535	545	555	565	575	585	595	605	615	625	Total.
515	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	1
525	...	...	...	...	2	...	...	...	...	...	...	...	...	...	...	...	...	2
535	1	1	...	...	1	1	1	...	...	...	...	...	...	...	...	...	...	5
545	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	1
555	...	...	...	1	1	1	...	...	1	...	...	...	...	...	...	...	...	4
565	...	...	...	...	2	1	1	...	...	...	...	...	...	...	...	...	...	4
575	...	...	...	...	1	1	...	1	...	1	...	...	...	...	...	...	...	4
585	...	...	...	1	1	2	1	2	...	...	...	...	...	...	...	...	...	7
595	...	...	...	...	...	1	...	1	1	1	...	...	...	...	...	...	...	4
605	...	...	...	...	1	...	...	2	...	...	...	...	1	...	...	...	...	4
615	...	...	...	...	...	1	...	...	1	...	...	...	1	...	...	...	...	3
625	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	1
Total	1	1	...	2	10	8	4	6	3	2	...	...	2	...	...	...	1	40

HEAD WIDTH RELATIVE TO CHEST WIDTH AT 14 DAYS OF AGE

[r=0.477±0.066]

Head width.	Chest width.									
	85	90	95	100	105	110	115	120	125	Total.
70	2	5	3	1	...	...	...	...	...	11
75	1	3	4	3	1	1	...	...	...	13
80	2	3	5	6	4	8	...	...	...	28
85	...	...	2	5	1	...	...	...	1	9
90	...	...	...	1	...	...	...	...	...	1
Total	5	11	14	16	6	9	...	...	1	62

HEAD WIDTH RELATIVE TO CHEST WIDTH AT 280 DAYS OF AGE

[r=0.69±0.064]

Head width.	Chest width.														
	135	140	145	150	155	160	165	170	175	180	185	190	195	200	Total.
90	...	...	...	...	...	1	...	...	...	...	...	...	...	...	1
95	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0
100	...	...	...	...	1	...	...	...	...	...	...	...	...	...	1
105	...	...	1	1	...	2	...	...	...	...	...	...	...	...	4
110	...	...	1	1	...	1	2	2	3	...	...	...	...	...	10
115	1	...	1	...	1	...	1	1	4	...	1	3	1	...	14
120	...	...	...	...	1	...	...	...	4	1	...	...	...	2	8
125	...	...	...	...	...	...	...	...	...	1	...	...	...	...	1
130	...	...	...	...	...	...	...	...	...	...	1	...	...	...	1
Total	1	...	3	2	3	4	3	3	11	2	2	3	1	2	40

TABLE III.—*Correlations between the body measurements of sheep*—Continued

LOIN WIDTH RELATIVE TO CHEST WIDTH AT 14 DAYS OF AGE.

[$r=0.699\pm0.044$]

Loin width.	Chest width.									
	85	90	95	100	105	110	115	120	125	Total.
60	4	2	3	....	....	....	....	....	....	9
65	1	7	7	3	....	....	....	....	....	18
70	....	2	2	7	2	....	....	....	....	13
75	....	....	2	2	4	7	....	....	....	15
80	....	....	....	3	....	2	....	....	1	6
85	....	....	....	1	....	....	....	....	....	1
Total	5	11	14	16	6	9	....	....	1	62

LOIN WIDTH RELATIVE TO CHEST WIDTH AT 280 DAYS OF AGE

[$r=0.62\pm0.066$]

Loin width.	Chest width.														
	135	140	145	150	155	160	165	170	175	180	185	190	195	200	Total.
95	....	....	1	....	....	....	....	....	....	....	....	....	....	....	1
100	....	....	2	....	....	....	....	....	....	....	....	....	....	....	2
105	....	....	....	....	....	....	....	....	....	....	....	....	....	....	0
110	....	....	....	....	2	2	....	....	....	....	....	....	....	....	4
115	....	....	....	2	....	1	2	....	3	....	....	....	....	....	8
120	1	....	....	....	....	1	1	1	5	....	....	1	1	....	11
125	....	....	....	....	....	....	....	1	1	2	2	1	....	1	8
130	....	....	....	....	1	....	....	1	1	....	....	1	....	1	5
135	....	....	....	....	....	....	....	....	....	....	....	....	....	....	0
140	....	....	....	....	....	....	....	....	1	....	....	....	....	....	1
Total	1	....	3	2	3	4	3	3	11	2	2	3	1	2	40

HEAD WIDTH RELATIVE TO LOIN WIDTH AT 14 DAYS OF AGE

[$r=0.363\pm0.074$]

Head width.	Loin width.						
	60	65	70	75	80	85	Total.
70	2	7	2	....	....	....	11
75	3	2	3	3	2	....	13
80	3	8	5	9	3	....	28
85	1	1	2	3	1	1	9
90	....	....	1	....	....	....	1
Total	9	18	13	15	6	1	62

TABLE III.—*Correlations between the body measurements of sheep*—Continued

HEAD WIDTH RELATIVE TO LOIN WIDTH AT 280 DAYS

[$r = 0.58 \pm 0.071$]

Head width.	Loin width.										
	95	100	105	110	115	120	125	130	135	140	Total.
90	....	....	....	....	1	....	....	....	....	....	1
95	....	....	....	....	....	....	....	....	....	....	0
100	....	....	....	1	....	....	....	....	....	....	1
105	....	1	....	1	1	1	....	....	....	....	4
110	1	....	....	1	4	3	1	....	....	....	10
115	....	1	....	....	1	5	2	4	....	1	14
120	....	....	....	1	1	2	3	1	....	....	8
125	....	....	....	....	....	....	1	....	....	....	1
130	....	....	....	....	....	....	1	....	....	....	1
Total	1	2	....	4	8	11	8	5	....	1	40

SUMMARY OF DATA ON CORRELATIONS BETWEEN BODY MEASUREMENTS

Age.	Dimension.	Mean.	Standard deviation.	Coefficient of variability.	Coefficient of correlation.	
Days.						
14	Trunk length	316.29	23.72	0.075	Head length—foreleg length.	0.443±0.068
280	do	523.75	28.91	.055	do	.693± .063
14	Head length	112.34	7.44	.066	Head length—trunk length.	.554± .059
280	do	176.50	12.51	.071	do	.537± .076
14	Foreleg length	262.58	18.55	.071	Foreleg length—trunk length.	.498± .064
280	do	384.50	19.23	.050	do	.700± .054
14	Hindleg length	297.10	23.29	.078	Hindleg length—trunk length.	.557± .074
280	do	441.50	25.06	.057	do	.474± .066
14	Chest depth	140.16	12.08	.087	Chest depth—trunk length.	.526± .062
280	do	259.63	14.97	.058	do	.544± .075
14	Height shoulder.	386.13	26.16	.066	Height—trunk length	.564± .058
280	do	573.25	28.54	.050	do	.609± .067
14	Head width	78.065	4.947	.063	Head width—chest width.	.477± .066
280	do	113.375	6.920	.061	do	.630± .064
14	Chest width	101.855	7.418	.072	Loin width—chest width.	.699± .044
280	do	170.000	15.49	.091	do	.620± .066
14	Loin width	69.348	6.380	.092	Head width—loin width.	.363± .074
280	do	119.125	8.795	.074	do	.580± .071

All correlation coefficients shown are positive, though this association in variation is never very close, only three of the correlations being as great as the smallest that Castle [1] found between skeletal dimensions in rabbits. The correlations at 14 days are both smaller and less uniform than at 280 days, indicating that animal proportions are more unstable at that immature age.

The smallest correlation at 280 days is between hindleg length and trunk length. It is questionable whether the hindleg length is a satisfactory character for this purpose because of the unavoidable erorrs in measurement, owing to the tendency of sheep to hunch down when handled, thereby producing fluctuations in measurement of material value. Except this case, the 280-day correlations show a range between extremes which is approximately equal to the range in correlations between the skeletal dimensions in rabbits shown by Castle, the range shown by Castle being from 0.658 to 0.858, and the range shown here being from 0.537 to 0.700. It is very probable that the higher degree of association between the variations in dimensions shown by castle is due to the greater accuracy that can be obtained in measuring prepared single bones than by measuring characters in live animals, such as are represented in this work, most of which involves dimensions of several bones.

The similarity in the ranges of correlations, however, indicates that it is true of sheep as Castle finds it of rabbits that

> to a large extent the factors which determine size are general factors affecting all parts of the skeleton simultaneously.

The foreleg length shows the highest correlation with other measurements. Its coefficient with head length is 0.693 and with trunk length it is 0.700.

The correlations between dimensions representing width are somewhat lower than this but fairly uniform. Since the growth curves (fig. 2) show that length dimensions attain full development somewhat earlier than dimensions of width, it is probable that, as width approaches maturity, its coefficients will more nearly approximate those of length, especially as the correlation does not seem to be as definite in the immature as in those approaching maturity.

[1] MacDowell, E. C. SIZE INHERITANCE IN RABBITS. With a preferatory note and appendix by W. E. Castle. Carnegie Inst. Washington. Pub. 196, p. 51. 1914.